

GLOBAL ANALYSIS OF THE POTENTIAL FOR N₂O PRODUCTION IN NATURAL SOILS

A. F. Bouwman,¹ I. Fung,²
E. Matthews,³ and J. John⁴

Abstract. A simple global model of the production potential of nitrous oxide (N₂O) in natural soils is developed to analyze the relative importance, both geographically and seasonally, of the different controls on N₂O production at the global scale. Five major controls on N₂O production are included: (1) input of organic matter, (2) soil fertility, (3) soil moisture status, (4) temperature, and (5) soil oxygen status. Indices for the controls are derived from global gridded (1°×1° resolution) data bases of soil type, soil texture, NDVI and climate. The model explains close to 60% of the variability found in measurements reported at about 30 sites in six different ecosystems throughout the world. Although this result is reasonable for global analyses, the correlation is considered insufficient to make global estimates of nitrous oxide emission with

confidence. The model confirms conclusions from earlier studies that the major source regions of nitrous oxide are in the tropics.

1. INTRODUCTION

Nitrous oxide (N₂O) is present in the atmosphere in trace quantities. Its concentration in 1990 was about 310 parts per billion by volume (ppbv), about 1000 times less than that of CO₂, and it is increasing at the rate of about 0.8 ppbv y⁻¹ [Watson et al., 1992]. The seemingly small growth rate, about 0.25% y⁻¹, is the result of a large imbalance (about 30%) between the sources and sinks [Prinn et al., 1990; Khalil and Rasmussen, 1992]. Despite its low abundance in the atmosphere, N₂O plays an important role. Its long lifetime of ~132 years [Isaksen et al., 1992] means the system has a long memory of its emission history. The radiative forcing of N₂O is, molecule for molecule, about 200 times that of CO₂ [Isaksen et al., 1992]. In the stratosphere the principal mechanism for N₂O destruction is by photolysis; in addition, N₂O is destroyed by reaction with excited oxygen atoms [Crutzen, 1976]. The latter reaction is the largest source of stratospheric NO (nitric oxide), initiating a complex set of gas phase reactions that lead to catalytic ozone destruction.

Neither the sources nor the causes for the increase in N₂O are well known. It is generally accepted that the most important source is natural soils, seconded by emissions from the oceans [Seiler and Conrad, 1987] although there is significant uncertainty regarding the distribution and magnitude of the sources themselves. For some time it was thought

¹National Institute of Public Health and Environmental Protection, Bilthoven, The Netherlands.

²NASA Goddard Space Flight Center, Institute for Space Studies, New York.

³Hughes STX Corporation, resident at NASA Goddard Space Flight Center, Institute for Space Studies, New York.

⁴Department of Applied Physics, Columbia University, resident at NASA Goddard Space Flight Center, Institute for Space Studies, New York.

that, like CO₂, the primary cause for the increasing concentration was combustion of fossil fuels, in particular, coalburning power plants producing electricity [Hao et al., 1987]. However, identification of an artifact in the flask sampling procedure ruled out combustion (including biomass burning) as the major cause of the trend [Muzio and Kramlich, 1988]. Minor sources identified so far include agricultural fields amended with nitrogenous fertilizers, animal manure, aquifers, sewage, industry, automobiles, biomass burning, land clearing, and trash incineration [Watson et al., 1992; Khalil and Rasmussen, 1992]. It is not clear if these sources can account for the secular trend.

In soils and aquatic systems, microbial processes are responsible for both the production and consumption of atmospheric nitrous oxide and nitric oxide. In vitro experiments demonstrate significant N₂O production by both denitrifiers [Firestone et al., 1980] and nitrifiers [Yoshida and Alexander, 1970; Blackmer et al., 1980; Lipschultz et al., 1981; Poth and Focht, 1985]. Recently, it was observed that N₂O may also be formed by other processes [Robertson and Tiedje, 1987; Tiedje, 1988], but the significance of these processes on a global scale, and their mechanisms and regulators, are poorly known.

Denitrification comprises the group of processes whereby nitrogenous oxides, principally nitrate (NO₃⁻) and nitrite (NO₂⁻), are reduced to dinitrogen gases (N₂), nitrous oxide and nitric oxide [Firestone and Davidson, 1989]. It occurs under oxygen-limited conditions; under strictly anaerobic conditions, nitrous oxide and nitric oxide may also serve as electron acceptors. Several processes, including abiotic ones, all match this definition [Firestone and Davidson, 1989]. Under natural conditions, the nitrate available for denitrification depends on the rate of nitrification [Myrold and Tiedje, 1985; Tiedje, 1988]. With relatively high nitrate supply, denitrification is related primarily to the amount of available organic compounds [Ottow et al., 1985] and N₂O production shows a strong positive correlation with both CO₂ evolution and available carbon [Eaton and Patriquin, 1989].

In nitrification, ammonia (NH₄⁺) is oxidized to nitrite (NO₂⁻) or nitrate (NO₃⁻). In natural soil ecosystems, the ammonia comes mainly from decomposition and mineralization of organic matter. Nitrogen inputs to natural ecosystems come from N deposition and biological dinitrogen fixation [Boring et al., 1988]. Major regulators of nitrification are temperature, oxygen, nutrient availability, carbon and nitrifiable N sources. Under oxygen-limited conditions, nitrifiers can use NO₂⁻ as a terminal electron acceptor to avoid accumulation of the toxic NO₂⁻, whereby N₂O is produced [Poth and Focht, 1985]. While denitrification is inhibited by oxygen, nitrification is an aerobic process. Therefore denitrification in constantly anaerobic systems is low since under such conditions, nitrification is blocked

by lack of oxygen [Sahrawat and Keeney, 1986; Bowden, 1986].

There is considerable controversy about the relative importance of nitrification and denitrification for N₂O production. Many researchers have suggested that nitrification is the major source of N₂O in "aerobic" agricultural soils [Ryden et al., 1978; Breitenbeck et al., 1980; Bremner and Blackmer, 1981; Klemmedtsson et al., 1988] and in natural semiarid "well aerated" soils [Anderson et al., 1988; Parton et al., 1988]. In peat sediments [Gordon et al., 1986], certain tropical forests [Livingston et al., 1988; Keller et al., 1988; Robertson and Tiedje, 1988] and some temperate forests [Eaton and Patriquin, 1989], denitrification may be the major process involved. Apparently, nitrification is a relatively constant process across ecosystems while denitrification rates are temporally and spatially variable [Firestone and Davidson, 1989].

Estimates of the annual N₂O release from natural soils illustrate the uncertainty about this source. The ranges are 7-16 Tg (Tg = 10¹²g) [Bowden, 1986], 3-25 Tg [Banin, 1986], 39 Tg [Seiler and Conrad, 1987], and 2.8-7.7 Tg [Watson et al., 1992]. Most of these studies rely on one or a few flux measurements, multiplied by areas of broad vegetation groups, to derive global emissions. These "representative measurement" approaches cannot explain the extreme variability of fluxes observed both in space and time. Fluxes of N₂O from temperate grasslands have been modeled extensively [e.g., Parton et al., 1988]; a model based on rainfall events and detailed description of microbiological and physical soil processes was developed by Li et al. [1992]. While conceptual models of nitrification and denitrification exist [e.g., Robertson, 1989; Firestone and Davidson, 1989; Davidson, 1991], extrapolation from site-specific measurements or models to regional or global emissions is a considerable challenge. Schimel et al. [1988] and Matson et al. [1989] stressed the need for stratification of ecosystems to describe the variability of environmental conditions responsible for N₂O fluxes: Matson and Vitousek [1990] stratified tropical forests primarily on the basis of soil fertility. Such approaches lead to better-justified regional estimates of N₂O emissions.

The global scale of the modeling presented here makes description of soil processes a difficult task. It is necessary to identify the major controls, and to describe and quantify their relative importance in a simple way. Our working hypothesis is that, since N₂O can be produced by both nitrifiers and denitrifiers, the potential for N₂O production in upland soils under natural conditions is related to the amount of nitrogen cycling through the soil-plant-microbial biomass system [Matson and Vitousek, 1987; Firestone and Davidson, 1989], hence to the N mineralization, nitrification, and denitrification rates

[Matson and Vitousek, 1987; Robertson and Tiedje, 1984; Martikainen, 1985]. In this "process pipe" or "hole in the pipe" concept [Firestone and Davidson, 1989; Davidson, 1991] the size of the holes or leaks in the pipe through which N₂O and NO escape is determined by factors that control the partitioning of the reacting N species to N₂O or more reduced/oxidized products. The rate at which N moves through the process pipe determines the importance of the leaks. This means that low denitrification rates lead to low trace gas release, regardless of the relative proportions of end products [Firestone and Davidson, 1989; Davidson, 1991].

We present a simple global model to analyze the geographic and seasonal variations of the various controls of N₂O production and their relative importance in the total annual emission. The focus is natural ecosystems, the largest single source term in the present-day N₂O budget. Given the paucity of available flux measurements, an immediate goal is to test the simple model of N₂O fluxes and to identify gaps where measurements and analyses are needed to reduce uncertainties about this source term.

The major controls on N₂O emissions in the model are discussed in section 2. The synthesis of these regulators into a simple schematic model for determining the N₂O emission potential is described in section 3. The one-dimensional model is applied at every 1°×1° gridbox globally. Modeled distribution of N₂O production potential and its sensitivity to the controlling factors are presented in sections 4.1 to 4.3. Regression relationships between modeled and observed N₂O emission values are presented in section 4.4, yielding an equation to translate the modeled non-dimensional N₂O potentials into dimensional fluxes (section 4.5). Global data sets of surface climate, soil properties, and satellite observations of the normalized difference vegetation index (NDVI), used to derive the geographic variation of the controls used in the model, are discussed in the appendix.

2. MAJOR CONTROLLING FACTORS OF N₂O PRODUCTION IN SOILS

The global model of N₂O production potential is based on the hypothesis that N₂O fluxes are directly related to the rate of nitrogen cycling through the soil-plant-microbial system. Hence we need to describe general patterns of decomposition and N mineralization, and, given the amount of N available in the soil, the major determinants of nitrification and denitrification.

Climate, vegetation, and soil are fundamentally interrelated to determine the ecosystem that develops in a particular area. The parent rock and soil type determine the type of vegetation via nutrient availability. Sites with low nutrient availability select for species with low nutrient demands

producing low-quality litter which decomposes slowly and further reduces nutrient availability [Anderson, 1992]. Soil properties are also molded by the vegetation, particularly the amount and nature of organic matter formed during decomposition of plant detritus. Soils can have low fertility for various reasons. Low pH causes low solubility of a number of major and minor trace elements while the solubility of other elements (e.g., aluminum) increases. Highly weathered soils of the tropics (e.g., Ferralsols and Acrisols) usually contain less phosphorous than younger, less weathered soils of the temperate regions; they may even show P-fixation [Jordan, 1985; Duxbury et al., 1989; Driessen and Dudal, 1991].

Decomposition rates [Jordan, 1985] and mineralization processes are closely related to soil fertility because of feedbacks between litter quality, decomposition rates and nutrient availability [Adams et al., 1970; Zimka and Stachurski, 1976; Miller, 1981; Vitousek, 1982]. In general, concentrations of all major nutrients, including nitrogen, in above-ground and belowground forest biomass are markedly higher in fertile soils than in poor ones [Vitousek and Sanford, 1986].

Decomposition and mineralization rates are determined also by litter properties, most notably lignin concentration and C/N ratios. With low lignin concentrations (~10-15%) decomposition rates can be predicted from nitrogen concentrations or C/N ratios, while with high lignin concentrations the lignin/N ratio or initial lignin determines decomposition [Anderson, 1992]. The C/N ratio of organic material supplied to the soil influences the amount of N immobilized in microbial biomass. This influences N availability which in turn may affect nitrification and denitrification activities and products of denitrification [see Ottow, 1985]. The low C/N ratio in tropical forests leads to rapid and more complete decomposition of organic matter inputs [Duxbury et al., 1989] and high N mineralization rates in these soils [Vitousek and Sanford, 1986].

Soil moisture and temperature control soil processes at all levels and are important factors governing the speed of organic matter decomposition. Because of year-round high temperatures, soil processes in the humid tropics can remain active throughout the year, and annual nutrient cycling can be faster than in regions where cold or drought interrupts these processes. Jenkinson and Ayanaba [1977] estimated that decomposition rates in the tropics are four times those in temperate zones, while decomposition in mediterranean regions has been found to be twice that in temperate climates [Oades, 1988]. Measurements of soil organic matter stocks and leaf litterfall suggest that decomposition rates mimic global patterns of temperature and moisture. Post et al. [1985] noted that the C/N ratio is generally lower

in warm climates. This is consistent with the observation that tropical forests generally cycle 2–4 times more nitrogen between soil and vegetation than do most temperate ecosystems [Vitousek, 1984; Jordan, 1985]. However, this may be caused by ecosystem characteristics other than temperature. Apparently, nitrogen is not limiting growth in these tropical systems but other nutrients, such as phosphorous in strongly leached soils, may be limiting [Vitousek, 1984]. Because of nitrogen limitation, temperate forests generally have higher C/N ratios in litter and slower N mineralization rates than do tropical forests [Robertson and Tiedje, 1984; Jordan, 1985; Vitousek and Sanford, 1986; Vitousek and Matson, 1988]. Fluxes in temperate forests are much lower than those in most tropical environments, which may be explained by lower N availability and less favorable moisture and temperature conditions.

Soil-water content is the balance of inputs from rainfall, leaching and capillary rise, and consumption by plants. It has been shown to influence N₂O emissions from well-drained soils [Mosier and Parton, 1985; Klemetsson et al., 1988; Groffman and Tiedje, 1988]. Aerobic microbial activity increases with soil-water content until water displaces air and restricts oxygen diffusion so that maximum rates of microbial respiration, nitrification and mineralization occur at the highest water content at which soil aeration remains nonlimiting. This critical water content is strongly dependent on soil texture. In general, microbial activity peaks at 60–80% of field capacity [Linn and Doran, 1984], the amount of water held at soil-water potentials of about 10 kPa (10 kPa = 0.1 bars). Nitrification and associated N₂O production also show maximum activity at 60–80% of field capacity [Greaves and Carter, 1920; Davidson, 1991].

Optimum conditions for denitrification may occur at water contents from 80% to over 100% of field capacity [Linn and Doran, 1984; Klemetsson et al., 1988]. There is, however, a clear hysteretic effect whereby respiration and denitrification rates slowly decrease monotonically during the drying phase [Groffman and Tiedje, 1988]. Soils close to saturation show low N₂O production [Davidson, 1991] because N₂O diffusion may be limited [Sahrawat and Keeney, 1986; Keller et al., 1986] resulting in a greater fraction of N₂O reduced to N₂. Uptake of N₂O from the atmosphere by wet soils may occur under very wet conditions [Ryden, 1981, 1983; Letey et al., 1981; Smith et al., 1983; Keller et al., 1986].

Wetting of dry soils causes pulses in N mineralization, nitrification and N₂O fluxes [Denmead et al., 1979; Letey et al., 1981; Mulvaney and Kurtz, 1984; Sextone et al., 1985; Mosier et al., 1981, 1986; Parton et al., 1988; Vitousek et al., 1990]. Letey et al. [1981] showed that release of N₂O from the soil to the atmosphere is enhanced by alternate drying and

wetting of soils although peaks in N₂O production may decline with subsequent wetting events.

Overall denitrification activity is strongly stimulated at low oxygen pressures [Colbourn and Harper, 1987; Firestone and Davidson, 1989] but associated N₂O fluxes are low under anaerobic conditions [e.g., Terry et al., 1981; Davidson, 1991]. Oxygen status of soils is controlled by the interplay between water inputs, oxygen supply, and oxygen consumption. Soil-water content is crucial as oxygen diffuses 10⁴ slower in water than in air [Nye and Tinker, 1977].

Soil oxygen is consumed by root respiration and microbial activity. Oxygen consumption by microorganisms is driven by the supply of carbon and, under dry conditions, by water as a stimulator of metabolic activity. Denitrification is often found in "hot spots" created by decomposing organic matter which generates anaerobic microsites [Dowdell and Smith, 1974; Duxbury et al., 1982; Parkin, 1987; Schmidt et al., 1988]. This phenomenon may explain some of the high spatial variability of soil denitrification commonly observed [Ryden et al., 1978; Rolston et al., 1978; Breitenbeck et al., 1980; Bremner et al., 1980; Mosier et al., 1981; Folgarunso and Rolston, 1984; Colbourn et al., 1984; Goodroad and Keeney, 1985; Colbourn and Harper, 1987].

A strong relationship exists between soil texture and denitrification activity [Groffman and Tiedje, 1989]. Fine-textured soils have more capillary pores within aggregates than do sandy soils, thereby holding soil water more tightly. As a result, anaerobic conditions may be more easily reached and maintained for longer periods within aggregates in fine-textured soils than in coarse-textured soils. Soil-drainage characteristics also influence denitrification activity [Colbourn and Harper, 1987; Groffman and Tiedje, 1989] by affecting soil aeration.

Studies on the effect of temperature on N₂O fluxes show Q₁₀ values of 5 at 10°C to 1.5 at 30°C [Mosier and Parton, 1985], 2.8 between 15° and 25°C [Denmead et al., 1979], 2.28 between 10° and 20°C, 1.99 from 20° to 30°C and 1.35 at 30° to 40°C [Blackmer et al., 1982]. Temperature may not control the release of N₂O in ecosystems where soil nitrogen temporarily accumulates due to wet-dry cycles or freeze-thaw cycles [Anderson and Poth, 1989]. Denitrification during early spring and autumn in temperate climates may account for a significant portion of the annual N₂O released [Keeney et al., 1979; Goodroad and Keeney, 1984a; Schmidt et al., 1988; Christensen and Tiedje, 1990].

Soil pH also has a marked effect on the products of denitrification. Denitrification rates are low under acid conditions and more rapid under slightly alkaline conditions, but the N₂O fraction may be larger at low soil pH [Focht, 1974; Goodroad and Keeney, 1984b; Martikainen, 1985; Eaton and Patriquin, 1989; Brumme and Beese, 1992].

particularly with an adequate nitrate supply. This is commonly attributed to the sensitivity of N₂O reductase to proton activity [Alexander, 1977]. Simply lowering soil pH does not always increase the N₂O ratio suggesting that the soil and its resident organisms, rather than pH per se, determine the N₂O fraction [Ottow et al., 1985]. This may be due to the observed apparent adaptation of strains of denitrifiers to low pH [Parkin et al., 1985].

3. MODEL DESCRIPTION

The following parameters were selected as control variables in the N₂O model: (1) input of organic matter (CARBON); (2) soil fertility (FERT); (3) temperature effect on organic matter decomposition and nitrogen mineralization (SOD); (4) soil-water availability affecting decomposition, mineralization and nitrification (H₂O); and (5) soil-oxygen limitation affecting denitrification (O₂).

We assume that organic matter input is proportional to litter amount which in turn is proportional to net primary productivity of the vegetation. The mobilization rate of nitrogen in organic matter is proportional to the rate of decomposition and mineralization as determined by soil temperature, soil moisture and soil fertility. We recognize that composition of the organic material is also an important determinant of decomposition rate. However, there is no global dataset or proxy dataset for lignin content or C/N ratios in litter, and so we have not included these controls explicitly. As C/N ratio may be related to temperature [Post et al., 1985] and soil fertility [Vitousek and Sanford, 1986], their effect on decomposition and mineralization rates may be indirectly captured by temperature (SOD) and fertility (FERT) factors.

Soil pH has also been identified as a regulator for N₂O production. Because global data on soil pH is lacking, this soil property is not included as a separate factor in this study. Instead, we assume that soil pH and soil fertility are closely related and hence complementary.

A central part of the model is a description of soil-water regulation of nitrification/denitrification. We use a bucket model of water balance, which includes variations in soil drainage and topsoil texture and determines monthly water status of the topsoil. If the soil-water status is high, there is high water availability and low oxygen availability - conditions favorable for denitrification. The model is described below and illustrated schematically in Figure 1. Three of the five regulators vary monthly: SOD, H₂O and O₂. The remaining two, FERT and CARBON, are constant through the year.

Because of the lack of quantitative relationships between N₂O fluxes and the various controlling parameters for soil types on a global scale, our strategy was to first translate ideas about relative importance into ranked nondimensional indices. The

indices range from 0 to 10 or from 1 to 5, with high numbers signifying importance for N₂O production. Such translations may be straightforward for numeric data such as temperature. For control factors such as soil fertility, a subjective ranking of soil units was carried out. The suite of control indices were then combined to form indices for N₂O fluxes.

The focus of the model requires data which are global in domain and which span at least a year. The finest spatial resolution of the primary data sets used is 1° latitude by 1° longitude, about 110 km × 110 km at the equator. For these reasons, the model cannot resolve episodic effluxes of N₂O after rainstorms, localized "hot spots" and high spring and autumn emissions in temperate ecosystems which are often reported. The importance of such high-frequency, local events in the global budget has not been established.

The primary gridded data bases on climate, soil type, soil texture, and vegetation are discussed in the appendix. The global distribution of soil groups is shown in Plate 1.

Input of organic matter (CARBON). Under natural conditions, litterfall and root decay are the major sources of carbon and nitrogen to the soil. Most ecosystems have abundant surface litter throughout the year. Therefore the seasonal variation of C and N mobilization in the litter is governed more by decomposition rates rather than by seasonal variations in litterfall. We assume that the geographic pattern of annual litterfall is the same as that of annual net primary productivity (NPP). NPP is the result of soil and environmental conditions, and for many temperate ecosystems also the result of nitrogen availability. Hence NPP may only be correlated indirectly to nitrogen.

The satellite-derived normalized difference vegetation index (NDVI; see appendix) has been shown to be a good correlate for NPP [Goward et al., 1986; Box et al., 1989]. The annual integral of the NDVI, rather than monthly NDVI values, is used because litterfall is asynchronous with productivity and with nitrogen mineralization and nitrogen may be immobilized in microbial biomass before it is liberated.

Monthly NDVI composites for 1984 are gridded at 1° resolution for the globe, and summed to produce the annual integral. Monthly NDVI values range from -0.1 to 0.5, and annual totals range from -0.1 to 4.0. For consistency with other factors used in the study, the NDVI totals are rescaled to range from 0 to 10, for the index CARBON (Plate 2). Use of the NDVI captures the variability of NPP at the same resolution as that of the soil data.

Soil fertility (FERT). In this study, soil fertility is the inherent capability of soil material to supply nutrients to plant roots [see Sanchez, 1976; Brady, 1976]. This definition excludes soil N availability which is a combined result of vegetation, climate,

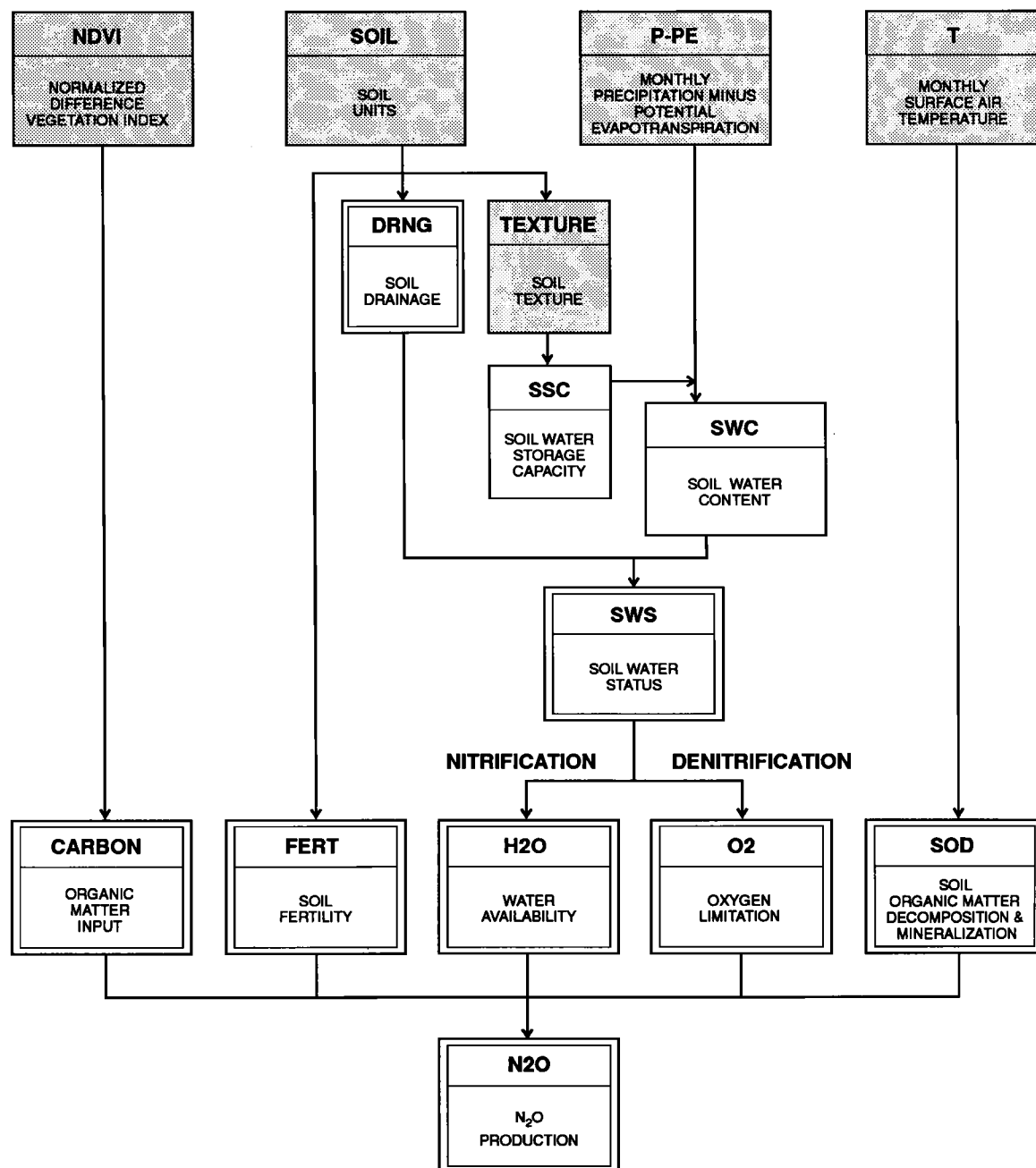


Fig. 1. Schematic diagram of the model of N₂O production. Shaded boxes denote input data and double-bordered boxes denote nondimensional indices.

and soil. With this definition, mineralization of nitrogen is indirectly determined by the combination of CARBON, FERT, SOD and H2O.

Soil characteristics important for inherent fertility are soil pH, cation exchange capacity, base saturation, and amounts of weatherable minerals; in some cases P fixation also plays a role. The scale for soil fertility is adapted from Food and Agriculture

Organization (FAO) [1981] for the major FAO/Unesco soil groups (Table 1); indices for some individual soil units within groups vary due to their diagnostic horizons or properties. For example, Nitols (Table 1, soil group 12) are highly fertile soils common to the tropics. Within the group of Nitols, the dystic Nitols are assigned a lower index because their base saturation is less than 49%

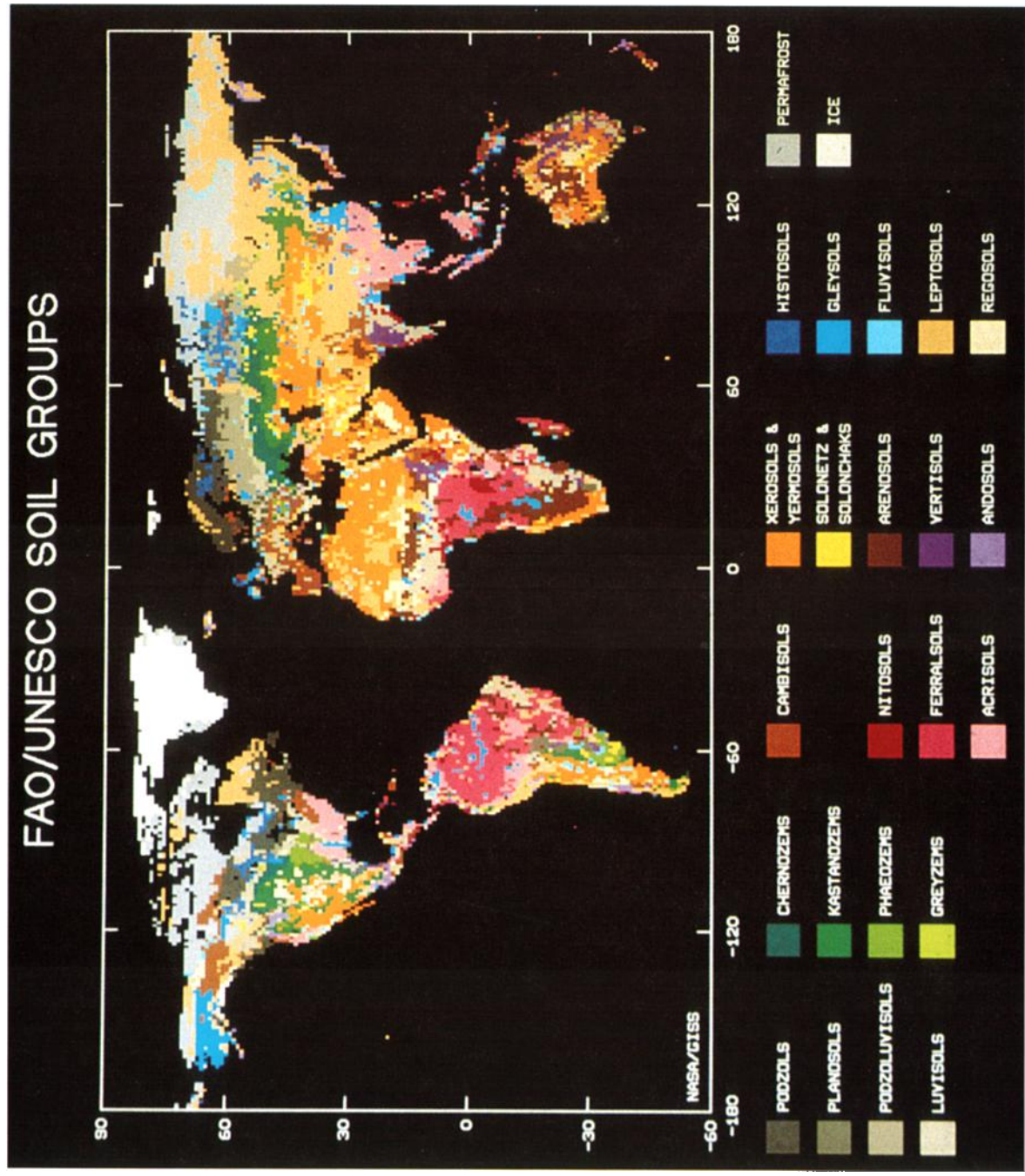


Plate 1. Distribution of major soil groups from the data set of Zobler [1986] digitized from FAO [1974-1981] soil maps. See Table 1 for descriptions.

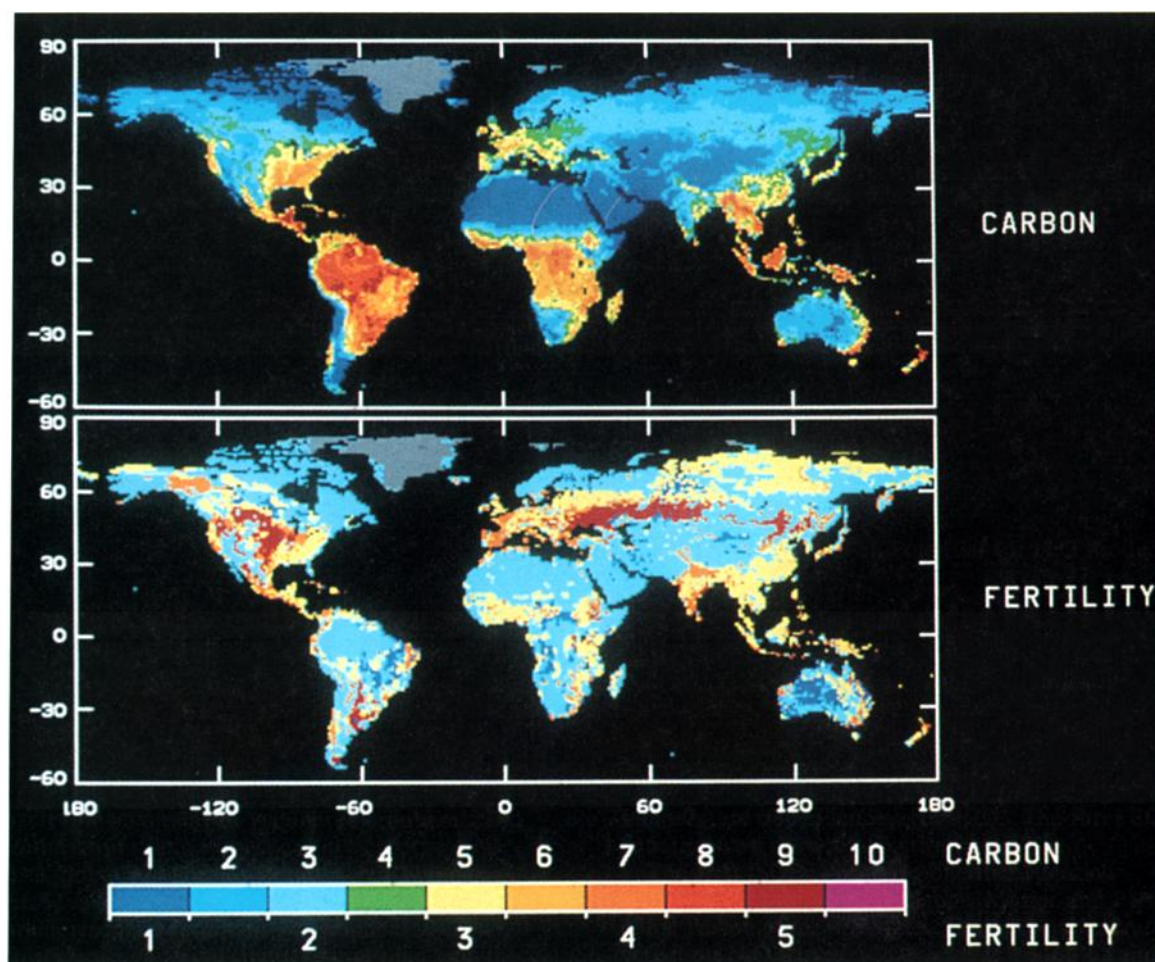


Plate 2. Distribution of factors used in the model: CARBON (upper panel), representing the input of organic matter, is NDVI scaled from 0–10, and FERT (lower panel), soil fertility, scaled from 1–5 (see Table 1).

of the cation exchange capacity [FAO/Unesco, 1974–1981]. In general, leached soils in wet climates have lower fertility than soils with a less pronounced downward flow of water over the year. Ferralsols (soil group 13) are strongly leached soils with variable charge characteristics, dominated by kaolinite and hydrated oxides of alumina and iron; their fertility is low due to low cation exchange capacity, the presence of alumina at the exchange complex, low content of weatherable minerals and phosphorous fixation. Podzols (soil group 2) are also infertile, generally because of low cation exchange capacity, low content of weatherable minerals and alumina saturation.

The global distribution of soil fertility index (FERT) is shown in Plate 2. Globally, soils are characterized predominantly by moderately low fertility: soils covering slightly more than half the ice-free land area have fertility indices of two. About one quarter of the land is of intermediate fertility, while the other fertility classes account for <10% each.

Temperature effect on rate of soil organic matter decomposition and N mineralization (SOD). Rates of decomposition and nitrogen mineralization are regulated by a number of soil factors including temperature, moisture, fertility, and texture. All these factors, except soil temperature, are represented in the factors H₂O and FERT. Lacking a global data set on soil temperatures, we use monthly climatologies of surface air temperature [Shea, 1986]; this might introduce timing errors of up to 1–2 months particularly in middle to high latitudes. In this study, we investigated three temperature dependencies for SOD. The three SOD functions are shown in Figure 2.

The first (SOD1) is an exponential function obtained for semiarid grasslands [Mosier and Parton, 1985; Parton et al., 1988] describing the temperature effect on N₂O fluxes: SOD1 = 10 at T = 50°C, and SOD1 = 0 for T < 0°C, with a rapid increase between 10° and 30°C. The second equation (SOD2) is a quadratic function adapted from Parton et al. [1987] describing decomposition of soil organic matter in

TABLE 1. Indices of Soil Fertility (FERT) and Drainage (DRNG) Assigned to Different Soil Units

	Soil Unit	FERT	DRNG	Area (10 ⁶ ha)
I	SOILS WITH PERMAFROST			674
1	Soils with permafrost within 200 cm			674
	gelic Cambisols	3	5	232
	gelic Gleysols	3	5	148
	gelic Histosols	2	5	66
	gelic Planosols	2	5	-
	gelic Regosols	2	5	228
II	SOILS CONDITIONED BY SUBHUMID CLIMATES			885
2	Soils with illuviation of organic matter and/or sesquioxides			493
	ferric Podzols	2	1	-
	gleyic Podzols	2	3	44
	humic Podzols	2	1	31
	leptic Podzols	2	1	19
	orthic Podzols	2	1	398
	placic Podzols	2	2	1
3	Soils with strong textural differentiation with slowly permeable subsoil			141
	dystic Planosols	1	3	1
	eutric Planosols	2	3	63
	humic Planosols	2	3	1
	mollic Planosols	2	3	16
	solodic Planosols	1	3	60
4	Soils with argic horizon* underlying a bleached subsurface horizon			251
	dystic Podzoluvisols	2	2	66
	eutric Podzoluvisols	3	2	159
	gleyic Podzoluvisols	3	3	26
III	SOILS CONDITIONED BY DRY SUBHUMID (SUB-) TROPICAL OR SUBHUMID TEMPERATE CLIMATES			950
5	Soils with argic horizon*			950
	albic Luvisols	3	2	114
	calcic Luvisols	4	2	63
	chromic Luvisols	4	2	249
	ferric Luvisols	3	2	264
	gleyic Luvisols	4	3	73
	orthic Luvisols	4	2	162
	plinthic Luvisols	3	4	23
	vertic Luvisols	4	3	2
IV	SOILS CONDITIONED BY STEPPE CLIMATES			897
6	Soils with argic horizon* and organic matter accumulation			27
	gleyic Greyzems	3	3	11
	orthic Greyzems	3	2	17
7	Soils with organic matter accumulation, annual precipitation > evapotranspiration			153
	calcaric Phaeozems	5	1	4
	gleyic Phaeozems	5	3	11
	haplic Phaeozems	5	1	58
	luvic Phaeozems	5	2	80
8	Soils with organic matter accumulation, annual precipitation = evapotranspiration			225
	calcic Chernozems	5	1	32
	glossic Chernozems	5	1	6
	haplic Chernozems	5	1	124
	luvic Chernozems	5	2	63

TABLE 1. (continued)

	Soil Unit	FERT	DRNG	Area (10 ⁶ ha)
9	Soils with organic matter accumulation, annual precipitation < evapotranspiration			492
	calcic Kastanozems	5	1	14
	haplic Kastanozems	5	1	225
	luvic Kastanozems	5	2	253
V	SOILS CONDITIONED BY LIMITED AGE			758
10	Weakly developed soils			758
	calcic Cambisols	4	1	86
	chromic Cambisols	3	1	81
	dystic Cambisols	3	1	245
	eutric Cambisols	4	1	230
	ferralic Cambisols	3	1	23
	gleyic Cambisols	3	3	15
	humic Cambisols	4	1	60
	vertic Cambisols	4	2	18
VI	SOILS CONDITIONED BY WET (SUB-) TROPICAL CLIMATES			2228
11	Leached soils with argic horizon*			903
	ferric Acrisols	3	2	164
	gleyic Acrisols	2	3	40
	humic Acrisols	3	2	41
	orthic Acrisols	3	2	576
	plinthic Acrisols	2	4	82
12	Strongly weathered soils with deeply developed argic horizon*			209
	dystic Nitisols	3	1	114
	eutric Nitisols	5	1	80
	humic Nitisols	5	1	15
13	Strongly leached soils dominated by hydrated oxides			1116
	acric Ferralsols	1	1	68
	humic Ferralsols	2	1	27
	orthic Ferralsols	2	1	506
	plinthic Ferralsols	1	4	38
	rhodic Ferralsols	2	1	73
	xanthic Ferralsols	2	1	404
VII	SOILS CONDITIONED BY (SEMI-)ARID CLIMATES			2108
14	Desert soils			1876
	calcic Xerosols	2	1	253
	calcic Yermosols	2	1	314
	gypsic Yermosols	2	1	69
	haplic Yermosols	2	1	743
	gypsic Xerosols	2	1	6
	haplic Xerosols	2	1	133
	luvic Xerosols	2	2	107
	luvic Yermosols	2	2	235
	takyric Yermosols	2	1	16
15	Saline and alkaline soils			232
	gleyic Solonchaks	1	3	27
	mollic Solonchaks	2	1	5
	orthic Solonchaks	1	1	92
	takyric Solonchaks	1	1	3
	gleyic Solonetz	1	4	1
	mollic Solonetz	2	3	29
	orthic Solonetz	1	3	75
VIII	SOILS CONDITIONED BY THEIR PARENT MATERIAL			1146
16	Heavy textured cracking soils dominated by clays with swell- shrink properties			314
	chromic Vertisols	3	3	205
	pellic Vertisols	3	3	109

TABLE 1. (continued)

	Soil Unit	FERT	DRNG	Area (10 ⁶ ha)
17	Soils formed in volcanic ash			111
	humic Andosols	4	1	20
	mollic Andosols	4	1	12
	ochric Andosols	4	1	27
	vitric Andosols	4	1	52
18	Weakly developed soils with sand texture			721
	albic Arenosols	1	1	19
	cambic Arenosols	2	1	316
	ferralic Arenosols	1	1	302
	luvic Arenosols	2	2	84
IX	SOILS CONDITIONED BY THEIR PHYSIOGRAPHIC POSITION			3377
19	Soils influenced by a floodplain regime			245
	calcaric Fluvisols	4	1	61
	dystic Fluvisols	3	1	35
	eutric Fluvisols	4	1	138
	thionic Fluvisols	1	5	11
20	Soils influenced by groundwater			412
	calcaric Gleysols	3	5	16
	dystic Gleysols	2	5	161
	eutric Gleysols	3	5	134
	humic Gleysols	3	5	27
	mollic Gleysols	3	5	72
	plinthic Gleysols	2	5	2
21	Leptosols (shallow soils, mostly <10 cm thick)			2273
	Lithosols	2	1	2224
	Rankers	1	1	3
	Rendzinas	3	1	46
22	Weakly developed soils formed in unconsolidated non-alluvial material			447
	calcaric Regosols	2	1	189
	dystic Regosols	1	1	87
	eutric Regosols	3	1	171
X	ORGANIC SOILS			172
23	Histosols (peat soils)			172
	dystic Histosols	1	5	125
	eutric Histosols	2	5	47

Low index values indicate low fertility and free drainage. Soil units are classified by soil groups (arabic numbers) and soil clusters (roman numbers); the areas of each unit is given in column 4, while those of each group and cluster are in column 5. Total ice-free land area is $13,195 \times 10^6$ ha. Land ice is 1666×10^6 ha.

* argic horizon = subsurface horizon with distinctly higher clay content than overlying horizon.

grasslands. The optimum (SOD2 = 10) is at $T = 33^\circ\text{C}$. To avoid negative values, SOD2 is set to zero at $T < 0^\circ\text{C}$ and at $T > 49^\circ\text{C}$. The third relationship (SOD3) is a set of linear functions for four broad ecosystem groups: broadleaf vegetation, needleleaf vegetation, grassland, and tropical vegetation. The functions are derived from observations of CO_2 evolution from soils and mean monthly temperature [Fung et al., 1987]: SOD3 = 10 at $T = 50^\circ\text{C}$. The different slopes of the four functions reflect the differences in litter composition for the broad biome

groups. For comparable temperature ranges, grassland, with a high fraction of easily decomposable detrital material, has a faster relative decomposition rate than that of needleleaf woody vegetation.

Differences between the SOD1 and SOD2 functions are minor: the most marked differences are expected in temperate climates with mild winters. At temperatures between 0° and 10°C , SOD2 yields the lowest values; in that temperature range, SOD3 gives much higher values than the other functions.

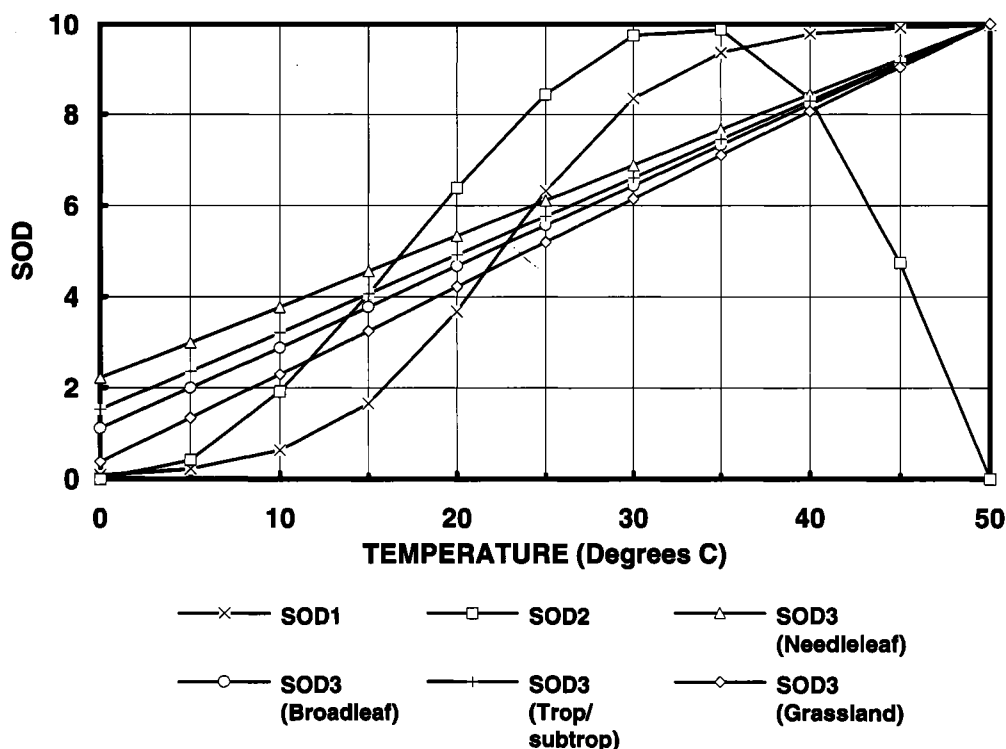


Fig. 2. Index of the rates of soil organic matter decomposition and N mineralization (SOD) as a function of temperature. SOD1 (reference) is taken from Mosier and Parton [1985] and Parton et al. [1988]; SOD2 from Parton et al. [1987]; SOD3 from Fung et al. [1987].

The three functions give similar results for the tropics. The SOD1 equation yields the best correlation with the measurement data (see Section 4.4). For that reason, SOD1 was chosen as the reference case. The global distribution of SOD1 is shown in Plate 3 (annual total of the monthly values).

Soil water and soil oxygen. A key to determining moisture conditions for decomposition and for distinguishing the pathways of nitrification versus denitrification is the degree of saturation and aerobicity of the soil which are determined by the soil water content (SWC) and its relation to the maximum amount of water held in the soil [soil water storage capacity, SSC], and by soil drainage properties. Topsoils are the primary sites for N₂O production since maximum microbial activity and the most intensive rooting occur in this soil layer. Nitrification may dominate in the upper few millimeters [Seiler and Conrad, 1981] while denitrification may dominate below, particularly during periods of high water content [Goodroad and Keeney, 1985]. Therefore, we consider the topsoil, i.e. upper 30 cm of soil, as the zone of N₂O production. Some physical properties in zones below 30 cm, that influence water and air movement in the topsoil, are included in the soil drainage characteristics.

Soil water storage capacity (SSC). Soil water storage capacity is the maximum amount of water

held in the upper 30 cm of the soil at field capacity (soil water potential of 10 kPa = 0.1 bar), i.e. when internal drainage and redistribution have ceased. In reality, redistribution of water after wetting is continuous and the field capacity is reached after prolonged periods if at all. Nevertheless, for the scale and purpose of this study, the above definition of SSC is appropriate.

SSC values are listed in Table 2. For most soils, water storage capacity is derived from soil texture based on average soil physical characteristics of major texture classes [Euroconsult, 1989; Landon, 1984]. The global distributions of soil texture and SSC are shown in Plate 4. For several soils with special physical properties influencing field capacity, alternative water storage capacities are assigned regardless of soil texture. These are discussed in some detail, since the soils involved cover about 30% of the ice-free land surface of the Earth.

Vertisols (Table 1) are cracking clay soils dominated by montmorillonitic clays with swell-shrink properties. Their water storage capacity may be lower than expected on the basis of their clay content because it is usually difficult to wet these soils. After the initial rain, infiltration rates may decrease as the clay swells and closes the cracks [see Blokhuis, 1991]. On the basis of these characteristics, Vertisols are assigned a low storage capacity similar to coarse- and medium-textured

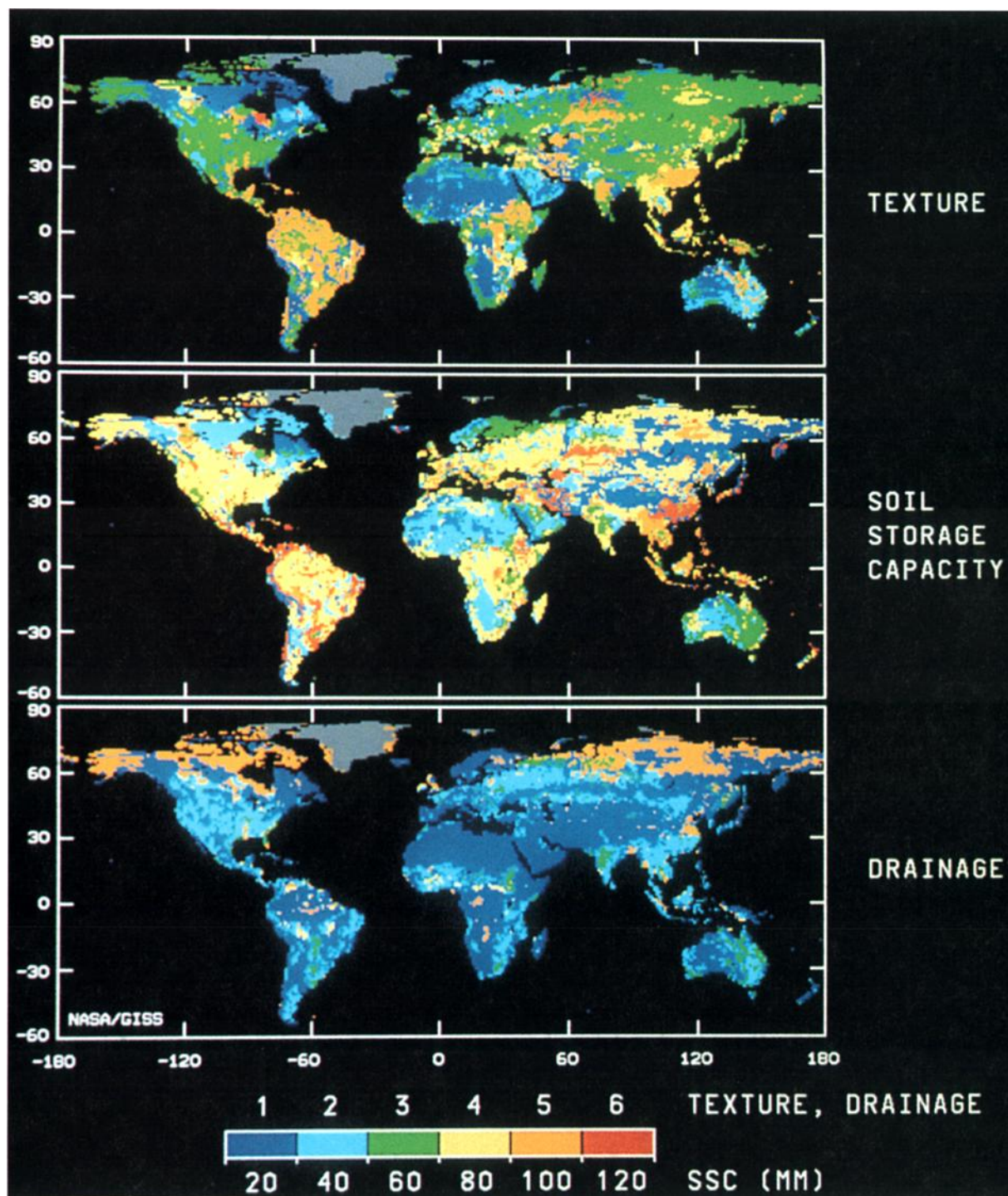


Plate 3. Distribution of soil characteristics derived from the soil data base. Texture class (upper panel) determines the soil storage capacity (SSC; middle panel). Refer to Table 2 for descriptions of numbered texture classes and soil storage capacity. Drainage indices (lower panel) for soil units are listed in Table 1.

TABLE 2. Soil Water Storage Capacity (SSC) of the Upper 30 cm

Texture Class	Soil Texture	SSC ^a	γ ^b	δ , ^b mm
1	coarse	40	15	0
2	coarse/medium	60	9	0
6	organic	60	18	0
3	coarse/fine	80	9	0
3	coarse/medium/fine	80	9	0
3	medium	80	9	0
4	medium/fine	100	9	0.1
5	fine	120	6	0.1
Soil Type ^c		SSC	γ ^b	δ , ^b mm
Rendzinas		15	15	0
Lithosols		15	15	0
Rankers		15	15	0
Vertisols		60	6	0.1
vertic Cambisols		80	9	0.1
Ferralsols		80	9	0
vertic Luvisols		80	9	0.1
Andosols		120	9	0

^a SSC is shown for major texture classes [Zobler, 1986] and for some soil types [FAO/Unesco, 1974-1981] with limited soil depth or clay minerals having specific soil-moisture retention characteristics. Based on Landon [1984] and Euroconsult [1989].

^b γ and δ are used in Eqn. (2) in the computation of transpiration and soil evaporation from the soil-water content; δ expresses the intercept of the soil-water extraction curve β .

^c A full list of soil units and their fertility and drainage indices is presented in Table 1.

soils. In addition, soil units with vertic properties are assigned SSC values similar to those of medium-textured soils.

Because particle size distributions of Andosols and Ferralsols are not easily determined [Dijkerman, 1991], texture information from the FAO/Unesco maps may be less reliable than for other soil groups. In Ferralsols, positively charged hydrated oxides and negatively charged kaolinite form stable aggregates with many biopores resulting in water retention characteristics similar to those of sands or medium-textured soils, although some Ferralsols are fine-textured. Ferralsols are assigned a water-storage capacity of 80 mm, equal to that of medium-textured soils.

Andosols are soils formed in volcanic ash, commonly with high aggregate stability. Water availability in Andosols is generally not lower, and is often higher, than in other mineral soil materials

[Van Reeuwijk, 1991], which may not be reflected by their texture. Therefore Andosols are assigned a topsoil storage capacity of 120 mm, equal to SSC values for fine textures.

Leptosols, shallow soils with a depth of ~10 cm or less, are assigned a low storage capacity of 15 mm since their shallowness is assumed to exert primary influence on water storage.

Soil water budget model. The monthly change in soil moisture is the difference between the supply, and demand of moisture at the surface. Supply is governed mainly by precipitation, while demand is governed by evaporation from soils and transpiration by plants.

Several soil moisture models are used in general circulation models, ranging from the simple bucket model of Manabe [1969], where SSC is uniformly 15 cm, to the simple biosphere model (SiB) of Sellers et al. [1986] and the complex biosphere-atmosphere scheme (BATS) of Dickinson et al. [1986] which take into account differential effects of biomes on soil-water balance. The recent models distinguish soil evaporation from plant evaporation and transpiration, as well as model explicitly vertical profiles of soil moisture. We note that in a bucket model where supply and demand are independent of soil moisture itself, the solution to the soil moisture equation is not uniquely determined; it is dependent on the initial soil water content assumed unless $SWC = 0$ or $SWC = SSC$ (runoff) sometime during the year.

We employed a simple soil-moisture model whose solution does not depend on an arbitrarily chosen initial condition. We adapted the Mintz and Serafini [1981] model for calculating monthly soil-water content. In this model, net supply is the difference between monthly precipitation (P_m) and evaporation from wet canopies (EI_m), while demand is the sum of transpiration through plants and evaporation from soils (ETS_m).

$$SWC_m = SWC_{m-1} + (P_m - EI_m) - ETS_m \quad (1)$$

Potential evapotranspiration (PE_m), maximum moisture demand by the atmosphere, is calculated from the surface air temperature according to Thornthwaite [1948]. Mean monthly surface air temperatures (T_m) and precipitation (P_m) are obtained from Shea [1986]. Three moisture regimes are considered, depending on the relation between precipitation and potential evapotranspiration:

$$\begin{aligned}
 P_m = 0 & \quad EI_m = 0 \\
 & \quad ETS_m = PE_m \times \beta_m \times \alpha \\
 P_m < PE_m & \quad EI_m = P_m \\
 & \quad ETS_m = (PE_m - P_m) \times \beta_m \times \alpha \\
 P_m \geq PE_m & \quad EI_m = PE_m \\
 & \quad ETS_m = 0
 \end{aligned} \quad (2)$$

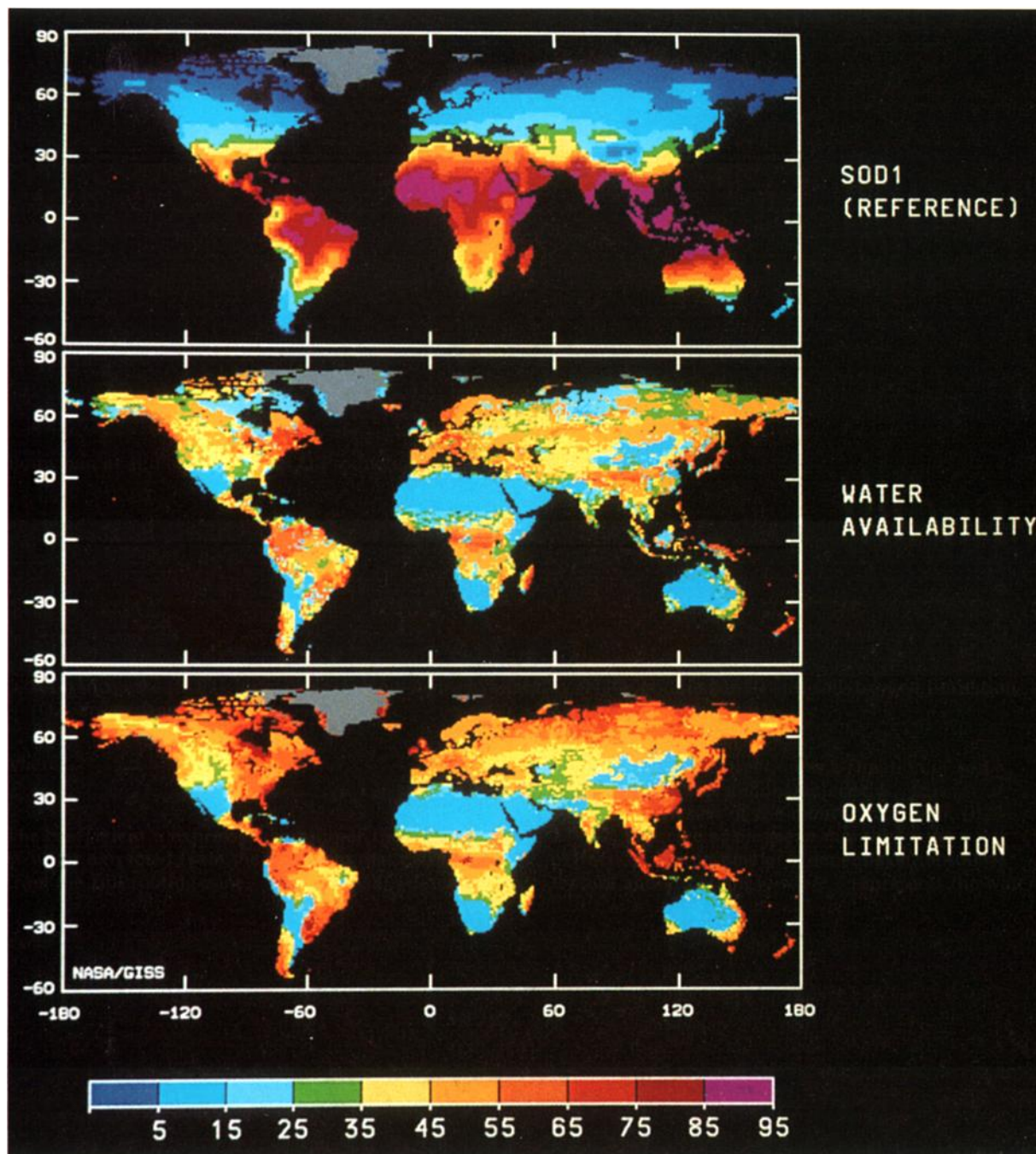


Plate 4. Distribution of annual sums of monthly indices for soil organic matter decomposition for the reference case (SOD1; upper panel), soil-water availability (H₂O; middle panel) and soil-oxygen limitation (O₂; lower panel).

where $\alpha = 0.4$ and

$$\beta_m = 1 - e^{-\gamma[(SWC_{m-1} + (P_m - EI_m)/2)/SSC - \delta]}$$

The coefficient α expresses the ratio of the amount of water extracted from the topsoil to that extracted from the full rooting zone. The function β describes

maximum water extraction as a function of soil water content and soil characteristics. It is calculated for 50% of the monthly addition, $(P_m - EI_m)/2$, to arrive at the mean monthly water extraction. Its parameter γ depends on topsoil texture and mineralogy, while δ represents the water

unavailable to plants, i.e. the intercept of the water extraction curve β . The values of δ and γ (Table 2) are based on Hillel [1980]. For clays, $\gamma = 6$, resulting in a strong decrease in water extraction below SWC/SSC about 50%. Due to the selected value of δ for clays, water extraction at SWC/SSC < 10% is reduced. In sands and medium-textured soils, β sharply decreases at values of SWC/SSC of about 40% and 20%, respectively. Because SWC is a function of β , the monthly equilibrium SWC is achieved independently of the initial water content at the start of the simulation.

Effects of Soil Drainage (DRNG). In the calculation of soil-water content above, drainage properties are not considered. Drainage is a soil property that determines the removal of excess water from the soil, and is an indicator of soil aeration. Soil drainage indices are used to estimate soil-water status and are prescribed for soil units on the basis of several soil properties including the presence of impermeable and less permeable horizons (Table 1). The global distribution of the drainage index (DRNG) is shown in Plate 4. We recognize that the soil data base may not represent the local spatial variations in drainage (see appendix), particularly for small areas of hydromorphic soils which may be important for N₂O fluxes.

Very poorly drained soils (DRNG = 5) include those soil groups strongly influenced by groundwater such as the Gleysols and Histosols, as well as soils with permafrost within 200 cm of the soil surface (gelic soil units). Soils with somewhat impeded drainage and moderately restricted aeration (DRNG = 4) include gleyic Solonetz and soils with plinthite; plinthic Acrisols and plinthic Ferralsols are wet tropical soils, usually with fluctuating water tables, and with firm plinthic subsurface layers within 50–125 cm of the surface that are iron-rich and humus-poor. Gleyic Solonetz are compact soils with hydromorphic properties and clay in the subsoil. The intermediate class (DRNG=3) indicates impeded drainage and restricted aeration; it encompasses gleyic soil units (in which only the subsoil is influenced by groundwater or with a seasonally perched water table within the profile), Planosols (a slowly permeable subsoil), Vertisols (soils with swell/shrinkage properties and montmorillonitic clays dominating the clay fraction) and the nongleyic Solonetz (compact alkaline soils with a natric horizon). About 20% of the land surface, with a drainage index of 2, comprises soils with an increase in clay content in the subsoil (argic horizon), [FAO/Unesco, 1988]. Water stagnation and anaerobic conditions may occur in these soils during periods of high precipitation. About two thirds of the land lacks the above properties and is considered freely drained (DRNG=1). The effects of drainage on soil oxygen limitation and water availability are difficult to quantify. The drainage indices are used to estimate soil water status.

Soil-Water Status (SWS). Soil-water status of the

TABLE 3. Scaled Soil-Water Status (SWS) as a Function of Soil Drainage (DRNG; see Table 1) and Modeled Soil-Water Content/Soil-Water Storage Capacity (SWC/SSC; see Table 2)

	SWC/SSC, %	Drainage Scale (DRNG)				
		1	2	3	4	5
1	0 - 20	1	1	1	1	2
2	20 - 30	2	2	2	2	3
3	30 - 40	3	3	3	4	5
4	40 - 50	4	4	4	5	7
5	50 - 60	5	5	5	6	8
6	60 - 70	6	6	6	7	9
7	70 - 80	6	7	7	8	9
8	80 - 90	7	7	8	9	10
9	90 - 100	7	8	9	10	10
10	surplus (>100%)	8	9	10	10	10

topsoil is scaled on the basis of soil-water content and drainage as shown in Table 3. Although it is difficult to combine drainage and soil-water status at their intermediate values in the index, we note several points: (1) distinguishing saturation levels <20% is not important; (2) we increase the SWS scale linearly up to the saturation; (3) we fill in the rest of the table by assuming that N₂O production likely asymptotes at high saturation and poor drainage. While it is clear that the highest SWS rank of 10 should be assigned to a poorly drained soil when the monthly soil-water content approaches storage capacity, the SWS scale is somewhat arbitrary. It represents a first attempt at quantifying our understanding of the effects of soil drainage characteristics on soil oxygen and soil moisture.

Effects of water status and oxygen status on decomposition, nitrification and denitrification. Two factors are derived to describe these effects: water availability (H₂O) and oxygen limitation (O₂). H₂O describes the influence of soil water on decomposition, mineralization and nitrification processes. In general, water contents of 60–80% of field capacity are favorable for these processes while nearly saturated and anaerobic soils have low H₂O values [Linn and Doran, 1984; Davidson, 1991]. H₂O (Table 4) is based on the soil-water status of the previous and current months. Wetting of dry soils is assumed to be more favorable, and drying soils less favorable, than are conditions of constant water content [Groffman and Tiedje, 1988]. Although we do not attempt to simulate the reported pulses in N₂O production after the wetting of dry soils, we hypothesize that pulses of N₂O at the onset of a wet season give a higher average monthly N₂O flux than in wet months preceded by moist conditions.

TABLE 4. Scaled Soil Water Availability (H₂O) for the Reference Case and Experiments 1–5 and 7

SWS in Preceding Month	SWS in Current Month									
	1	2	3	4	5	6	7	8	9	10
1	<u>1</u>	2	4	6	9	10	10	10	6	1
2	1	<u>1</u>	3	5	8	9	10	10	6	1
3	1	1	<u>2</u>	4	7	8	9	10	5	1
4	1	1	2	<u>4</u>	7	8	8	8	4	1
5	1	1	2	4	<u>6</u>	7	7	7	3	1
6	1	1	2	4	6	<u>7</u>	7	6	2	1
7	1	1	2	4	6	7	<u>7</u>	6	2	1
8	1	1	2	4	5	6	6	<u>5</u>	2	1
9	1	1	2	3	4	6	6	4	<u>2</u>	1
10	1	1	2	3	4	5	6	4	2	<u>1</u>

H₂O is a function of soil-water status (SWS, see Table 3) of the current month and of the preceding month. The H₂O scale corresponding to SWS in the current month only, used in experiment 6, is given by the underlined numbers on the diagonal of the table (see Table 5).

The regulator O₂ expresses effects of soil-oxygen status on denitrification. It is obtained from the soil-water status of the previous and current months (Table 5) and includes the effect of wetting and drying of soils. Oxygen limitation at soil-water contents of 60–80% is treated as most favorable for N₂O production by nitrification while denitrification is more prominent at water contents of >80%. In general, high levels of wetness result in greater oxygen limitation; wetting of dry soils is assigned higher O₂ indices than constantly wet or moist soils. The information in H₂O and O₂ is very similar at SWC values between 7 and 9. Under saturated conditions, low H₂O counteracts high O₂ values reflecting the simultaneous occurrence of conditions favorable for denitrification (O₂), and unfavorable for NH₄⁺ oxidation by nitrification. In one sensitivity experiment, only the current month determines H₂O and O₂; in that case the H₂O and O₂ scales are the diagonals in Tables 4 and 5, respectively. Annual sums of monthly H₂O and O₂ are shown in Plate 3.

N₂O production (N₂O). The controls on N₂O fluxes identified above are combined to yield monthly nondimensional N₂O indices at 1° resolution for the globe. We recognize that the five factors chosen are not independent. In particular, CARBON, scaled from the annual integral of the NDVI, captures geographic variations in temperature, soil moisture, and soil fertility.

There are many ways to combine the factors. Lacking information about relative importance, we

TABLE 5. Scaled Oxygen Limitation (O₂) for the Reference Case and Experiments 1–5 and 7

SWS in Preceding Month	SWS in Current Month									
	1	2	3	4	5	6	7	8	9	10
1	<u>1</u>	1	1	4	6	8	10	10	10	10
2	1	<u>1</u>	1	4	6	8	10	10	10	10
3	1	1	<u>1</u>	3	5	7	9	10	10	10
4	1	1	1	<u>3</u>	4	6	8	9	10	10
5	1	1	1	2	<u>3</u>	5	7	8	9	10
6	1	1	1	1	2	<u>4</u>	6	7	8	9
7	1	1	1	1	2	3	<u>5</u>	6	7	8
8	1	1	1	1	2	3	4	<u>5</u>	6	7
9	1	1	1	1	2	3	4	5	<u>6</u>	7
10	1	1	1	1	2	3	4	5	6	<u>7</u>

O₂ is a function of the soil-water status (SWS, see Table 3) of the current month and of the preceding month. The O₂ scale used in experiment 6, which is a function of SWS in the current month only, is given by the underlined numbers on the diagonal of the table.

assume that all five controlling factors are of equal importance, i.e. the maximum fertility factor has the same effect as the maximum oxygen limitation factor as far as N₂O production is concerned. Hence, although FERT is scaled from 1 to 5 because of our inability to discriminate further, FERT is multiplied by two (FERT*) to normalize to the other factors.

We model the nondimensional monthly N₂O production as the geometric mean of the five controlling factors. In this way, a low value for one of the factors automatically lowers the N₂O production index. For example, values of 1 and 9 for two factors are given less weight than 5 and 5, which yields the same arithmetic mean.

It is difficult to rank the above regulators a priori since the influences of these regulators varies among habitats [Tiedje, 1988]. Therefore the monthly nondimensional N₂O production index, N₂O is calculated for the reference case as:

$$N_2O = [O_2 \times H_2O \times SOD \times FERT^* \times CARBON]^{1/5} \quad (3)$$

where N₂O, O₂, H₂O, and SOD are indices calculated monthly, and FERT* and CARBON are site characteristics constant for every month. Under conditions where soil processes are inactive (months in which mean surface temperatures < 0°C), N₂O is set to zero. N₂O is also set to zero for months in which the monthly precipitation ≤ 5.0 mm and the soil-water content is ≤ 1%. When there is rainfall (P > 0) and the water budget equation predicts a dry

TABLE 6a. Mean and Standard Deviation of Modeled N₂O by Soil Group in the Tropics and Subtropics for the Reference Case and Seven Sensitivity Experiments

Soil Group	Area 10 ⁶ ha	REF	E1	E2	E3	E4	E5	E6	E7
2A	15	50 (19)	48 (21)	49 (21)	52 (25)	52 (22)	61 (20)	50 (20)	60 (33)
3A	95	38 (28)	35 (34)	33 (29)	39 (30)	41 (28)	45 (29)	38 (28)	69 (34)
5A	546	44 (26)	41 (33)	43 (25)	38 (32)	49 (25)	44 (26)	43 (27)	54 (43)
7A	15	53 (21)	56 (30)	51 (19)	45 (28)	56 (17)	48 (28)	53 (22)	73 (33)
9A	75	39 (35)	38 (43)	36 (36)	31 (44)	48 (30)	31 (38)	38 (36)	60 (42)
10A	290	53 (25)	53 (29)	53 (25)	49 (30)	58 (22)	50 (28)	53 (26)	61 (37)
11A	736	52 (15)	52 (18)	50 (16)	50 (18)	54 (17)	56 (17)	52 (15)	74 (25)
12A	204	58 (18)	56 (23)	57 (16)	52 (22)	64 (16)	52 (17)	57 (19)	66 (29)
13A	1113	56 (16)	52 (16)	51 (16)	60 (16)	59 (15)	58 (13)	56 (17)	82 (18)
14A	1008	12 (87)	10 (105)	12 (86)	10 (93)	14 (90)	14 (80)	12 (86)	11 (134)
15A	84	24 (41)	19 (59)	25 (35)	25 (46)	25 (39)	29 (53)	24 (41)	26 (87)
16A	281	39 (19)	36 (21)	42 (16)	35 (22)	41 (18)	36 (28)	37 (19)	35 (52)
17A	49	53 (29)	54 (31)	53 (30)	46 (36)	59 (27)	48 (33)	53 (29)	59 (29)
18A	696	25 (50)	22 (60)	24 (45)	27 (60)	28 (46)	31 (47)	25 (50)	34 (77)
19A	132	48 (39)	47 (44)	49 (38)	43 (44)	52 (37)	45 (43)	47 (40)	51 (49)
20A	162	45 (21)	42 (22)	44 (20)	43 (24)	45 (21)	55 (22)	45 (21)	64 (38)
21A	752	23 (78)	21 (89)	21 (76)	21 (86)	24 (78)	26 (74)	22 (78)	27 (106)
22A	330	18 (65)	15 (75)	19 (58)	17 (71)	21 (62)	22 (59)	18 (64)	16 (107)
23A	39	43 (17)	38 (16)	39 (17)	45 (17)	38 (21)	66 (16)	43 (17)	64 (33)

Standard deviations are in parentheses and are expressed as a percent of the mean N₂O index of each soil group for each experiment.

soil at the end of that month (SWC = 0), the soil has not been dry throughout the month. In that case the indices for O₂ and H₂O are low, giving low N₂O.

4. RESULTS AND DISCUSSION

The model was run globally at 1° resolution for 12 months. Model results for the reference case are discussed in section 4.1; sensitivity experiments analyzing the relative importance of the five factors are discussed in 4.2, and results for selected sites are

described in section 4.3. Results are compared with measurements in section 4.4 and used to estimate a global flux in section 4.5.

4.1. Global Results for the Reference Case

The mean annual sum of N₂O and its standard deviation (expressed as percentage of the mean) is presented for the reference case and the experiments for the 23 soil groups (Table 6). The standard deviation reflects the variation in annual sums over

TABLE 6b. Like Table 6a, but for Temperate and Subpolar Latitudes

Soil Group	Area 10 ⁶ ha	REF	E1	E2	E3	E4	E5	E6	E7
1B	674	3 (106)	9 (42)	3 (106)	2 (117)	3 (102)	3 (99)	3 (106)	7 (61)
2B	478	10 (64)	25 (45)	9 (72)	9 (79)	10 (62)	12 (62)	10 (62)	22 (60)
3B	46	29 (29)	36 (24)	26 (26)	30 (33)	29 (26)	35 (31)	29 (29)	57 (36)
4B	251	10 (32)	21 (28)	10 (33)	9 (36)	11 (33)	10 (30)	11 (33)	21 (33)
5B	404	22 (48)	37 (35)	21 (47)	19 (49)	24 (45)	20 (44)	23 (45)	40 (45)
6B	27	11 (24)	22 (18)	11 (23)	10 (23)	13 (19)	11 (22)	12 (25)	23 (20)
7B	138	31 (48)	48 (33)	30 (44)	25 (53)	34 (42)	27 (48)	32 (46)	52 (43)
8B	225	15 (23)	25 (29)	16 (22)	11 (24)	17 (20)	13 (23)	15 (24)	21 (30)
9B	417	15 (43)	25 (46)	17 (35)	11 (47)	18 (42)	14 (35)	16 (42)	21 (69)
10B	468	21 (63)	38 (52)	21 (62)	18 (69)	23 (62)	19 (58)	22 (62)	36 (62)
11B	166	36 (27)	54 (13)	32 (29)	34 (30)	37 (26)	36 (32)	36 (27)	72 (20)
12B	5	52 (23)	66 (9)	45 (26)	47 (26)	53 (26)	44 (29)	52 (22)	79 (23)
13B	3	49 (12)	56 (10)	43 (14)	48 (16)	48 (8)	46 (15)	50 (11)	76 (18)
14B	868	15 (46)	19 (54)	16 (48)	12 (57)	16 (49)	16 (43)	15 (45)	15 (75)
15B	148	16 (58)	19 (56)	17 (52)	16 (64)	16 (52)	16 (71)	16 (58)	19 (102)
16B	33	38 (22)	45 (16)	37 (18)	34 (26)	37 (18)	37 (30)	37 (23)	54 (45)
17B	62	23 (65)	50 (34)	23 (62)	20 (70)	24 (63)	20 (67)	24 (65)	43 (62)
18B	25	18 (55)	25 (39)	18 (51)	17 (63)	19 (57)	21 (48)	19 (51)	25 (74)
19B	114	16 (82)	25 (67)	16 (79)	12 (93)	17 (79)	14 (73)	15 (80)	21 (86)
20B	250	14 (77)	24 (58)	13 (83)	11 (88)	13 (72)	14 (85)	14 (76)	24 (77)
21B	1521	9 (86)	18 (67)	8 (92)	7 (101)	9 (81)	11 (78)	9 (86)	16 (83)
22B	117	18 (50)	27 (40)	18 (50)	15 (58)	20 (48)	18 (45)	18 (48)	24 (58)
23B	133	7 (58)	15 (42)	7 (61)	7 (60)	7 (51)	9 (56)	7 (58)	17 (48)

the areal extent of each soil group. Note that the SOD1 function is used in all cases. The results for the soil groups are presented separately for the tropics (Table 6a; within 30° of the equator) and the extratropics (Table 6b; poleward of 30° latitude). The annual sum of monthly N₂O indices for the

reference case is shown in Plate 5; the latitudinal and seasonal distribution of N₂O is shown in Figure 3. Since the index can range from 0 to 10 in any month, the potential annual maximum is 120, although the actual maximum is 84. The results for the reference case suggest that the wet tropics and

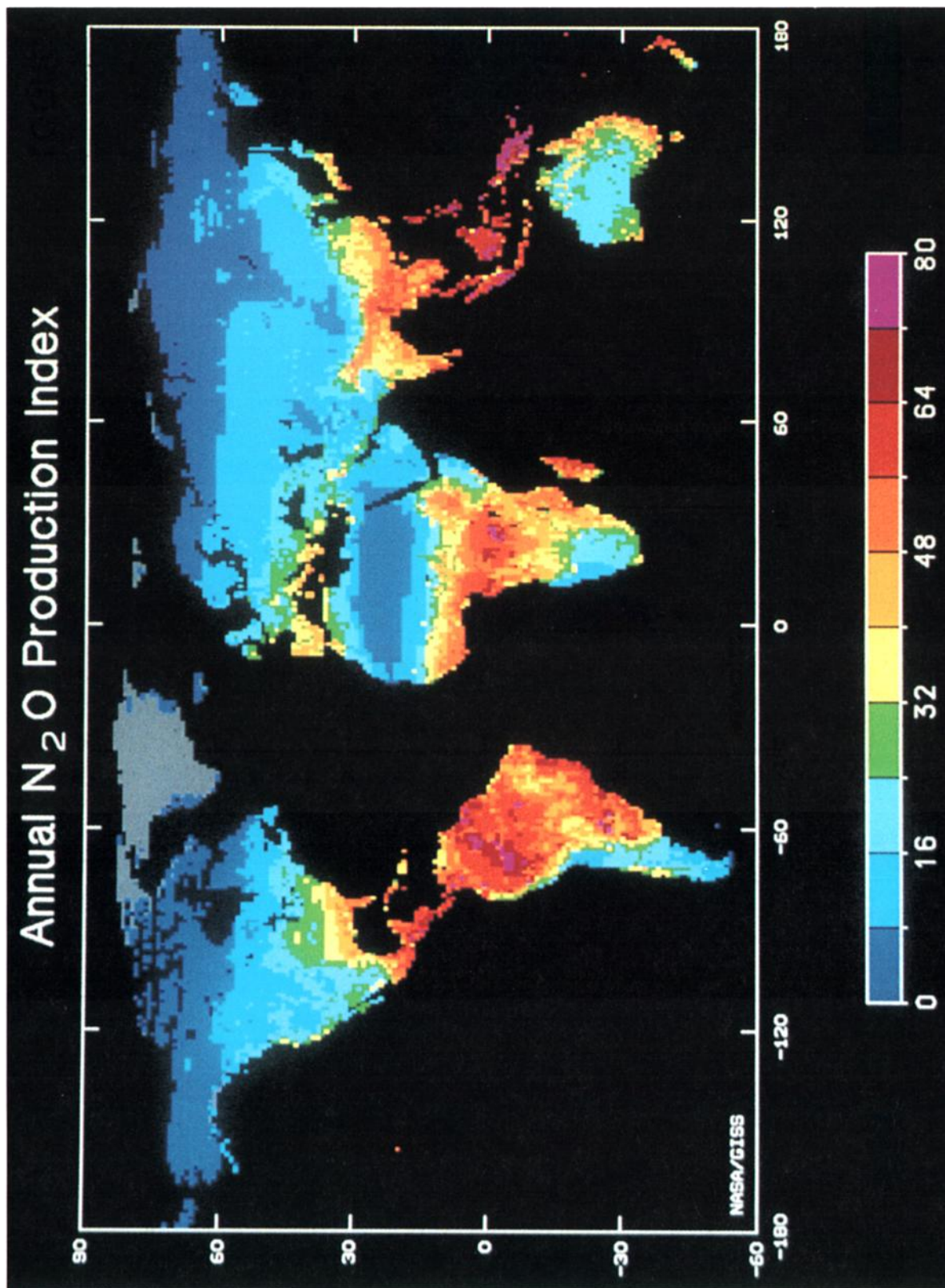


Plate 5 Distribution of annual sum of monthly N₂O production potential N₂O.

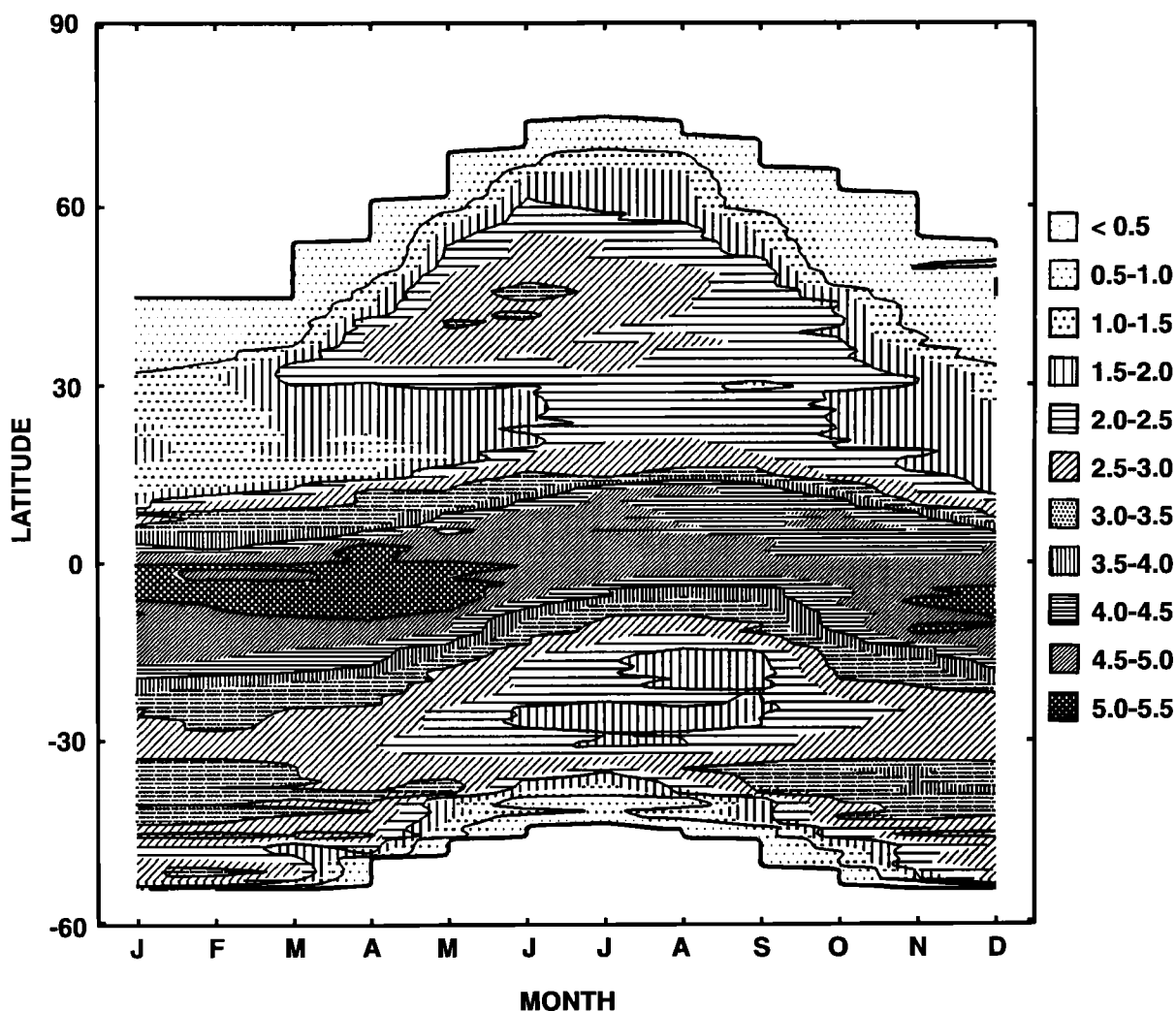


Fig. 3. Seasonal and latitudinal distribution of the N₂O production potential (N₂O). The zonal means are calculated over land areas.

subtropics have the highest levels of N₂O production. Mediterranean regions have intermediate values and soils in cold temperate and boreal regions, as well as deserts, have the lowest potential for N₂O production.

The most important soil group, in terms of areal extent and nitrous oxide production, is the Ferralsols (Table 1, group 13; Table 6a, group 13A). Because of their occurrence in somewhat drier climates, Acrisols (group 11) show slightly lower N₂O than do Ferralsols, while the fertile Nitisols (group 12) have higher values than Ferralsols. The extensive subtropical and tropical Luvisols (Table 6a, group 5A) also exhibit high N₂O potential. Other soils with high N₂O levels, but occupying minor areas, are tropical Podzols (group 2A), Vertisols (group 16), Andosols (group 17), Fluvisols (group 19) and Gleysols (group 20). The subtropical Phaeozems and

Kastanozems (groups 7A and 9A, respectively), occurring mainly in South America, exhibit high N₂O indices but their global effect is moderated by their small areas. Their temperate counterparts (Table 6b, groups 7B and 9B) show much lower N₂O levels. Another soil group of significant area is the shallow Leptosols (group 21). The model predicts that temperate Leptosols, when covered by their natural forest vegetation, have very low N₂O production, while tropical Leptosols are intermediate. About 15% of the Earth's ice-free land area is covered by desert soils (group 14) which have low potential for N₂O production mainly due to precipitation limitation. Tropical organic soils (group 23) show much higher N₂O values than their temperate counterparts.

Generally where N₂O is low, percent standard deviations are high, although the absolute standard

deviation may be low. The low annual N₂O values of temperate areas have higher percent standard deviations than do the tropics even when occupied by the same soil. Highest standard deviations are found in both tropical and temperate extents of groups 14 (desert soils), 15 (saline and alkaline soils), 18 (sand soils), 21 (shallow soils), and 22 (weakly developed soils), (Table 1, Plate 1). Percent standard deviations are small for the temperate and tropical distributions of Vertisols (group 16).

Temporal variability (not shown in Table 6) is expectedly high for temperate soil groups because of effects from seasonal temperature and moisture regimes. Very high intra-annual variabilities are also found for soils in semiarid and arid climates (soil groups 14–15) in both the tropics and temperate zones presumably due to precipitation fluctuations. N₂O indices vary seasonally for soils conditioned by parent material (groups 16–18) and for soils conditioned by their physiographic position (groups 19–22) but this variability is probably induced by the occurrence of these soils over a broad climatic range. Tropical and subtropical soils of wet climates (groups 11–13), show muted variations in N₂O during the year.

Figure 3 shows the seasonality of N₂O potential modeled in this study. Expectedly, the seasonal variation is greatest for temperate climates of the northern hemisphere; the seasonal variation in temperate climates of the southern hemisphere is about half that in the north. Tropical soils are active nitrous oxide sources throughout most of the year. Moreover, monthly N₂O values are higher for most of the tropics than for temperate climates; annual N₂O sums can be a factor 3–4 higher in the tropics than in temperate zones. These broad-scale patterns from a simple model agree with variations in decomposition rates and amounts of carbon and nitrogen cycling through soils in tropical and temperate climates [Jenkinson and Ayanaba, 1977; Vitousek, 1984].

4.2. Sensitivity Experiments

Characteristics of the sensitivity experiments are briefly described in Table 7. Annual N₂O production potential for the sensitivity experiments are shown in Table 6.

Experiment 1 (– SOD). In temperate climates, this experiment yields much higher values for annual N₂O than those of the reference case by removing temperature limitations in autumn, winter and spring (Table 6b). In the tropics, the experiment gives somewhat lower N₂O values (e.g., Table 6a, soil groups 12A and 13A) than the reference case. The role of SOD is also expressed by differences in the variability between the reference case and experiment 1. The spatial variability as expressed by the percent standard deviation decreases considerably for most extratropical soils when SOD

is excluded (except for the semiarid Kastanozems and desert soils – Table 6b, groups 9B and 14B, respectively). For most tropical soil groups, the percent standard deviation is higher in experiment 1 than in the reference case.

Experiment 2 (– CARBON). For nearly all tropical and temperate soils, this experiment yields N₂O values lower than those of the reference case. Results differ from the reference case most markedly in the wet tropics and subtropics, particularly for the Ferralsols (group 13). Over the distribution of these soils, exclusion of CARBON causes an average decline of 5 in the annual mean N₂O potential. In this experiment higher N₂O values are calculated for temperate soil groups 8B and 9B (steppe soils), 14B and 15B (desert soils) and for some minor tropical soil groups (15A, 16A, and 22A). The effect of excluding CARBON is minor in semiarid, arid, and steppe areas because other factors limit N₂O production. In the desert soils (group 14) and temperate steppe soils, N₂O is low in both the reference case and experiment 2 due to moisture limitations.

The results of experiments 1 and 2 indicate that SOD and CARBON are driving N₂O production in wet and moist tropics. Input of organic matter plays a less important role in temperate climates, because the annual N₂O is primarily determined by low temperatures in winter; and in dry climates, where soil moisture is the major regulator. These observations agree with the suggestion that carbon nowhere really prevents denitrification [Tiedje, 1988].

Excluding CARBON decreases the spatial variability for most temperate and tropical soil groups conditioned by their parent material (soil groups 15–18), but has no major effect on the variability in tropical soils in wet climates (Table 6a, groups 11A–13A). Exclusion of CARBON decreases the variability over tropical shallow soils (group 21A), whereas the variability increases for temperate zone distributions of these soils (group 21B). In the major climate-conditioned temperate soils (groups 3B–9B) exclusion of the organic input lowers spatial variability.

Experiment 3 (– FERT). Exclusion of soil fertility strongly reduces the annual N₂O for most highly fertile soils in temperate and tropical zones, for example, the Phaeozems, Chernozems, Kastanozems, and Nitosols (groups 7, 8, 9 and 12, respectively) and increases N₂O for the infertile tropical soils (group 2A, 3A, 13A, 15A, 18A, and 23A in Table 6a). For other temperate and tropical soils with intermediate soil fertility, the effect of experiment 3 is minor. Excluding soil fertility increases the standard deviation for most temperate and tropical soil groups due to the simplicity of the fertility scale in which the same index is associated with most soil units within each group. However, within landscapes, soil fertility may be a major cause

TABLE 7. List of Experiments to Evaluate the Sensitivity of the N₂O Production Index to Different Controls

Experiment	Description
Reference case:	all 5 factors are used; SODI is from Mosier and Parton [1985] $N_2O = \frac{\Sigma(O_2)^{1/5} \times (H_2O)^{1/5} \times (SOD)^{1/5} \times (FERT^*)^{1/5} \times (CARBON)^{1/5}}{1 \text{ y}}$
Experiment 1 (- SOD)	as reference case, but SOD is excluded $N_2O = \frac{\Sigma(O_2)^{1/4} \times (H_2O)^{1/4} \times (FERT^*)^{1/4} \times (CARBON)^{1/4}}{1 \text{ y}}$
Experiment 2 (- CARBON)	as reference case, but CARBON is excluded $N_2O = \frac{\Sigma(O_2)^{1/4} \times (H_2O)^{1/4} \times (SOD)^{1/4} \times (FERT^*)^{1/4}}{1 \text{ y}}$
Experiment 3 (- FERT)	as reference case, but FERT* is excluded $N_2O = \frac{\Sigma(O_2)^{1/4} \times (H_2O)^{1/4} \times (SOD)^{1/4} \times (CARBON)^{1/4}}{1 \text{ y}}$
Experiment 4 (- O ₂)	as reference case, but O ₂ is excluded $N_2O = \frac{\Sigma(H_2O)^{1/4} \times (SOD)^{1/4} \times (FERT^*)^{1/4} \times (CARBON)^{1/4}}{1 \text{ y}}$
Experiment 5 (- soil variability)	as reference case, but CARBON is excluded and the soil parameters are equal for all soils: FERT = 3, DRNG = 1, and texture is fine. This experiment studies the effect of climate on the variability of N ₂ O $N_2O = \frac{\Sigma(O_2)^{1/4} \times (H_2O)^{1/4} \times (SOD)^{1/4} \times (FERT^*)^{1/4}}{1 \text{ y}}$
Experiment 6 (H ₂ O and O ₂ of current month only)	as reference case, but soil-water and oxygen status in the preceding month is not considered. H ₂ O and O ₂ are the diagonals of Table 4 and 5, respectively.
Experiment 7 (only CARBON)	CARBON is used to predict N ₂ O $N_2O = \frac{\Sigma(CARBON)}{1 \text{ y}}$

FERT* = 2 × FERT, the fertility index from Table 1. See text for explanation.

of variability in N₂O fluxes [Table 8; Livingston et al, 1988; Matson et al. 1990].

Experiment 4 (- O₂). The O₂ factor provides information not included in the other four factors over the whole range of temperate and tropical ecosystems. Under wet conditions, high O₂ raises the levels of expected denitrification. Similar conditions produce low H₂O values simulating blockage of nitrification. Hence, because of the partial overlap of the scales of O₂ and H₂O, important effects on overall levels of N₂O in this experiment are found only in well-drained soils. No effect, or a decrease relative to the reference case, is found for the poorly-drained Gleysols and Histosols (soil groups 20 and 23, respectively). Where aerobic conditions prevail, O₂ depresses the N₂O index (Table 5). In most tropical and temperate soils, annual N₂O calculated in experiment 4 is higher and variability is lower than in the reference case, in agreement with Tiedje [1988], who concluded that in

aerobic systems, oxygen is the principal factor limiting denitrification.

Experiment 5 (- soil variability - CARBON). In experiment 5, CARBON is excluded and for all soils FERT = 3, DRNG = 1 (well drained) and texture is fine (high soil-water storage capacity). This eliminates variability produced by soil and vegetation differences and isolates the spatial variability caused by climate. The results can best be compared with experiment 2 (- CARBON). Smoothing soil differences increases spatial standard deviations for about half of the temperate soil types (Table 6b, groups 3B, 7B, 8B, 11-13B, 15-17B, 20B) and for most tropical soil groups (Table 6a). Tropical soils showing lower variability in this experiment are groups 12A-14A and 21A-23A. What this means can best be illustrated for the Ferralsols (group 13A), the major tropical soil group. These soils occur in relatively uniform climates so soil differences contribute to the variability. The

TABLE 8. Summary of Measurements of Nitrous Oxide Fluxes From Natural Ecosystems and the Corresponding Site Information

Vegetation Type/Ecosystem	Pa	Ta	Soil Texture	DC	pH	Nitrification, μg N/d/g soil	Flux μg N m ⁻² h ⁻¹		Month of Measure- ment	Soil Information and Location; Where Known, FAO/Unesco [1974-1981] and USDA [1975] classifications are given (USDA in parentheses)		Ref. ^a
							Range	Mean				
Temperate Regions, Nonwetland Sites												
Grasslands												
Native shortgrass prairie	300		fine loamy	wd ^b				9.6	5-9	Xerosol (ustollic Haplargid), Colorado		1 ^c
Native shortgrass prairie	300		15% clay (slope)	wd ^b				0.9	1 y	Xerosol (ustollic Haplargid), slope, Colorado		2 ^c
Native shortgrass prairie	300		28% clay (bottom)	wd ^b				1.8	1 y	Kastanozem (aridic Argiustoll), swale, Colorado		2 ^c
Grass			loam	wd ^b			0.5-2.5	1.5	>1 y	loess soil, Mainz, Germany		3
Native prairie	232 ^d		loamy sand	wd ^b	6.7		0.4-1.8	0.7 ^b	9-3	Wisconsin		4 ^c
Prairie	232 ^d		sand	wd ^b	6.2		0.4-2.1	0.5 ^b	9-3	Arenosol (typic Udipsamment), Wisconsin		4
Prairie	274 ^d		silt loam	wd ^b	7.3		0.4-3.2	0.7 ^b	9-3	lithic Chernozem (lithic Haplustoll), Wisconsin		4 ^c
Tall grass prairie, burned	600-800 ^b	10 ^b			6.0		2.2, 2.2 ^e		6-10, 4-10	loess over glacial till, Wisconsin		5
Tall grass prairie	600-800 ^b	10 ^b			6.0		2.5, 2.2 ^e		6-10, 4-10	loess over glacial till, Wisconsin		5 ^c
Grass (meadow)			sand				2.0-13.0		>1 y	Mainz, Germany		3
Grass (wet meadow)	600-800 ^b	10 ^b		pd ^b	6.1		30.6, 30.6 ^e		6-10, 4-10	Wisconsin		5
Deciduous forests												
Mixed forest				wd ^b			1.0-3.0		>1 y	loess soil, Mainz, Germany		3 ^c
Deciduous forest	900 ^b	13 ^b						10.3	1 y	mineral soil, New York		6
Hardwood forest	1300	6-13 ^d				13 kg ha ⁻¹ y ⁻¹		2	summer	soils in glacial till, New Hampshire		7
Oak			sandy loam	wd ^b	3.7 ^f		4.5-10.5 ^g	8.5	1 y	brown sandy soil, 7.2% C, Mainz, Germany		8
Oak			sandy loam	wd ^b	3.6 ^f		3.5-9.5 ^g	7.8	1 y	Podzol (Spodosol), 1-3 cm litter, 2.8% C, Mainz, Germany		8
Oak-hornbeam			sandy loam	wd ^b	3.7 ^f		5.5-7.5 ^g	7.7	1 y	Podzol (Spodosol), 1-2 cm litter, 2.4% C, Mainz, Germany		8

TABLE 8. (continued)

Vegetation Type/Ecosystem	Pa	Ta	Soil Texture	DC	pH	Nitrification, $\mu\text{g N/d/g soil}$	Flux $\mu\text{g N m}^{-2}\text{h}^{-1}$	Month of Measurement	Soil Information and Location; Where Known, FAO/Unesco [1974-1981] and USDA [1975] classifications are given (USDA in parentheses)	Ref. ^a
Oak-hornbeam			sandy loam	pd ^b	3.4 ^t		5.5-7.5 ^s	1 y	pseudogley, 1-3 cm litter, 3.4% C; Mainz, Germany	8
Hornbeam-oak			sandy loam	wd ^b	4.7 ^t		1.5-3.5 ^s	1 y	eutric Cambisol (typic Dystrochrept), 2.8% C, Mainz, Germany	8 ^c
Hornbeam-oak			sandy clay loam	wd ^b	6.7 ^t		2.5-4.5 ^s	1 y	eutric/dystic Cambisol (typic/dystic Eutrochrept), 3.6% C, Mainz, Germany	8 ^c
Black oak					5.0		5.4, 15.5 ^c	6-10, 4-10	Wisconsin	5 ^c
Black oak, 80 y			sandy loam	wd	sl. acid ^b		-0.01-0.56	1 y	Podzol/Cambisol (entic Haplorthod), stony, 5.2-7.8 cm litter, Mass.	9 ^c
Coniferous forests										
Red pine, 62 y			sandy loam	wd	sl. acid ^b		-0.08-0.42	1 y	Podzol/Cambisol (entic Haplorthod), stony, 4.3-4.9 cm litter, Mass.	9
White pine, 40 y	600-800 ^b	10 ^b			4.5		27.7, 36.4 ^c	6-10, 4-10	Wisconsin	5
Temperate Regions, Wetland Sites										
Forest, organic soil			organic	pd			11.4	1 y	Florida Everglades	6 ^c
Marsh (sedge meadow)			organic	pd	7.0		0.7, 1.1 ^c	6-10, 4-10	Wisconsin	5
Salt marsh (sp. alterniflora)			organic	pd			3.5	1 y	Louisiana	10 ^c
Brackish marsh (sp. patens)			organic	pd			5.4	1 y	Louisiana	10 ^c
Fresh marsh (Panicum hemitomon)			organic	pd			6.3	1 y	Louisiana	10 ^c
Open water, salt							1.1	1 y	Louisiana	10
Open water, brackish							2.4	1 y	Louisiana	10
Open water, fresh							3.9	1 y	Louisiana	10
Marsh, drained	600-800 ^b	10 ^b	organic	wd	6.1		64.8, 148.7 ^c	6-10, 4-10	Wisconsin	5

TABLE 8. (continued)

Vegetation Type/Ecosystem	Pa	Ta	Soil Texture	DC	pH	Nitrification, μg N/d/g soil	Flux μg N m ⁻² h ⁻¹		Month of Measure- ment	Soil Information and Location; Where Known, FAO/Unesco [1974-1981] and USDA [1975] classifications are given (USDA in parentheses)		Ref. ^a
							Range	Mean				
Tropical Regions, Nonwetland Sites												
Savannas												
Savanna (grassland/woodland)	1000	15-20 ^b	sandy loam/sand	wd ^b	<6 ^c		2.0-6.4	4	2	dry season, Venezuela		11 ^{ab}
Savanna (grassland/woodland)	1000	15-20 ^b	sandy loam/sand	wd ^b	<6 ^c			17	2	watered soil, Venezuela		11 ^{ab}
Undisturbed forests												
Terra firme moist forest	2000	25.8		wd ^b				43	4	Ferralsol (Oxisol), Manaus, Brazil		7 ^c
Terra firme moist forest	2000	25		wd ^b				13	12	Ferralsol (Oxisol), Manaus, Brazil		12 ^c
Terra firme moist forest	2000	24		wd ^b				31	3	Ferralsol (Oxisol), Manaus, Brazil		12 ^c
Primary tropical moist forest	4300	22		wd ^b				8	7	Tena, Ecuador		12 ^c
Elfin cloud forest		19		wd ^b				11	4	Puerto Rico		12 ^c
Colorado/Palm forest		20		pd				3	4	Puerto Rico		12
Primary forest	4100	25				0.16-2.14	29-52	40	10	Old alluvial, La Selva, Costa Rica		13 ^c
Primary forest	4100	25				0.14-2.10	7-25	16	10	Old alluvial, La Selva, Costa Rica		13 ^c
Primary forest	4100	25				1.42-2.16	14-32	23	10	Soils formed in basalt, La Selva, Costa Rica		13 ^c
Primary forest	4100	25				1.37-1.67	41-83	62	10	Soils formed in basalt, La Selva, Costa Rica		13 ^c
Primary forest	4100	25				2.44-3.62	12-24	18	10	Soils formed in basalt, La Selva, Costa Rica		13 ^c
Primary forest	4100	25				2.21-2.73	37-61	49	10	Soils formed in basalt, La Selva, Costa Rica		13 ^c
Primary forest, 75 y	2700	22		wd ^b		1.88-24.6	9-43	26	7	Andosol (Andept), Turrialba, Costa Rica		13 ^c

TABLE 8. (continued)

Vegetation Type/Ecosystem	Pa	Ta	Soil Texture	DC	pH	Nitrification, $\mu\text{g N/d/g soil}$	Flux $\mu\text{g N m}^{-2}\text{h}^{-1}$		Month of Measurement	Soil Information and Location; Where Known, FAO/Unesco [1974-1981] and USDA [1975] classifications are given (USDA in parentheses)		Ref. ^a
							Range	Mean				
Lowland forest, undisturbed	2200	25		wd ^b			15-35		1 y	Ferralsol (Oxisol), Manaus, Brazil		14 ^c
Terra firme forest	1770	26	clay	wd ^b	4.0	1.88-2.44	9.4-12.6	11.0	8	ridge, Ferralsol/Acrisol (Oxisol/Ultisol), Amazonia, Brazil		15 ^c
Terra firme forest	1770	26	clay	wd ^b	4.0	1.42-1.66	8.7-13.3	11.0	8	slope, Ferralsol/Acrisol (Oxisol/Ultisol), Amazonia, Brazil		15 ^c
Campinarana forest	1770	26	sand ^b	pd ^b	3.7	0.49-0.73	8.3-11.7	10.0	8	valley, Podzol/Arenosol (Spodosol/Psamment), Amazonia, Brazil		15
Terra firme forest	2200	25	clay	wd ^b		1.02-1.20		19	4-5	Ferralsol (Oxisol), Manaus, Brazil		16 ^c
Terra firme forest	2200	25	sand	wd ^b		0.05-0.09		3	4-5	Arenosol (Psamment), Manaus, Brazil		16
Primary montane forest	2200	16		wd ^b		-0.04		0	1	Andosol (Andept), 200 y, Hawaii		13
Primary montane forest	2200	16		wd ^b		-0.04	0.4-2.0	1.2	1	Andosol (Andept), 200 y, Hawaii		13
Primary montane forest	3500	16		wd ^b		0.06-0.18	0.5-1.7	1.1	1	Andosol (Andept), 1000 y, Hawaii		13
Primary montane forest	3500	16		wd ^b		-0.04-0.1	1.3-3.9	2.6	1	Andosol (Andept), 1000 y, Hawaii		13
Primary montane forest	4500	16		wd ^b		-0.11-1.07	1.0-2.6	1.8	1	Andosol (Andept), 4000 y, Hawaii		13
Secondary forest, logged	2000	26		wd ^b				23.1	7-8	Ferralsol (Oxisol), Manaus, Brazil		18 ^c
Dry tropical forest	748	25		wd ^b				9.1	9	Cambisol (Entisol), Chamela, Mexico		17 ^c
Dry tropical forest	748	25		wd ^b				2.0	3	Cambisol (Entisol), Chamela, Mexico		17 ^c

TABLE 8. (continued)

Vegetation Type/Ecosystem	Pa	Ta	Soil Texture	DC	pH	Nitrification, µg N/d/g soil	Flux		Month of Measure- ment	Soil Information and Location; Where Known, FAO/Unesco [1974-1981] and USDA [1975] classifications are given (USDA in parentheses)	Ref. ^a
							µg N m ⁻² h ⁻¹ Range	Mean			
Disturbed forests											
Secondary forest, 20 y	4200	25				1.92-2.56	4-52	28	10	Recent alluvial, La Selva, Costa Rica	13
Secondary tropical moist forest		22		wd ^b				7.4	7	Ecuador	12
Tabanuco forest, secondary		23		wd				42.5	4	Acrisol (Ultisol), Puerto Rico	12
Mahogany plantation		30		wd ^b				7.9	4	Puerto Rico	12
Lowland forest, cleared, burned	2200			wd ^b			15-35		1 y	Ferralsol (Oxisol), Manaus, Brazil	14
Tropical Regions, Wetland Sites											
Varzea	2200	25		pd			0.26-0.34	1	4-5	waterlogged, Gleysol (?), Manaus, Brazil	16 ^c

Pa = mean annual precipitation (mm); Ta = mean annual temperature (°C); DC = drainage class; wd = well drained; pd = poorly drained.

^a 1, Mosier et al. [1981]; 2, Parton et al. [1988]; 3, Seiler and Conrad [1981]; 4, Cates and Keeney [1987]; 5, Goodroad and Keeney [1984a]; 6, Duxbury et al. [1982]; 7, Keller et al. [1983]; 8, Schmidt et al. [1988]; 9, Bowden et al. [1990]; 10, Smith et al. [1983]; 11, Hao et al. [1988]; 12, Keller et al. [1986]; 13, Matson and Vitousek [1987]; 14, Luizao et al. [1989]; 15, Livingston et al. [1988]; 16, Matson et al. [1990]; 17, Vitousek et al. [1990]; 18, Keller et al. [1988].

^b Interpretations: A. F. Bouwman.

^c Measurements used in the comparison with modeled N₂O.

^d During measurements.

^e First value refers to summer/autumn 1979; second value to summer/autumn 1980; no annual figures available.

^f Soil pH measured in KCl solution.

^g 50% probability with 95% confidence range.

^h For the dry season, measurement data were compared with the modeled N₂O value averaged for May-October; for the rainy season, measurement data for the watered soil were compared with the modeled N₂O values averaged for November-May.

high spatial variability within soil groups 15A–B to 22A–B, soils conditioned by factors other than climate, reflects the distribution of these soils over different climatic zones. As in the reference case and experiment 1, the percent standard deviation among temperate soil groups is higher than in most of the equivalent tropical soils.

Experiment 6 (not considering soil water and oxygen of the previous month). Effects of wetting and drying are excluded in this experiment; H₂O and O₂ indices are given by the diagonals in Tables 4 and 5, respectively. The overall effect of considering water status only of the current month is minor and effects do not show patterns specific to soil groups or clusters. However, seasonal N₂O patterns exhibit a response. Results for selected sites (section 4.3) illustrate cases in which monthly N₂O indices are equal to those of the reference case (e.g., the Brazilian site). However, in sites with marked seasonality of rainfall, experiment 6 exhibits lower N₂O values at the onset of the wet season and higher values at the end of the growing period. The net result is no, or only minor, differences in the annual sum. For most soil groups conditioned by climate, spatial variability declines slightly in temperate regions (Table 6b, groups 2B, 5B, 7B, 9B, 10B, 12B–14B) and increases in the tropics (Table 6a).

Experiment 7 (only CARBON). Using CARBON as the sole predictor of N₂O production generally yields higher values than the reference case. Exceptions are tropical desert soils, Vertisols and Regosols (groups 14A, 16A, and 22A, respectively). N₂O increases are largest in temperate soils and in soils of the wet tropics. Standard deviations in experiment 7 are generally elevated for the tropical soils. Among temperate soil groups, variability is both higher and lower than in the reference case suggesting no clear relation with climate.

The CARBON factor represents organic matter inputs and not N inputs. In addition, CARBON includes much but not all information needed to characterize conditions responsible for N₂O production. In particular, soil aeration (drainage and soil wetness), soil–water availability, and possibly soil fertility, are probably not captured by the NDVI. Another problem of the underlying NDVI data is that NPP is overestimated in a number of ecosystems, particularly needleleaved forests and vegetation types with a strong seasonal pattern in growth [Box et al., 1989]. The broad spatial patterns and overall levels of CARBON are, however, very similar to the distribution of N₂O values from the reference case.

4.3. Results for Selected Sites

We selected four sites to discuss more fully. They are distributed throughout a range of climatic and ecological regimes and include locations representative of globally important soil groups, as

well as regimes dominated by various factors in the model, for example, water balance, temperature, soil fertility. One site represents a semiarid temperate climate, the second a humid temperate site, and two tropical sites include a seasonal climate and a per-humid climate. In the following discussions, the three functions describing soil organic matter decomposition (SOD) discussed above are referred to in abbreviated form as follows: SOD1, Mosier [from Mosier and Parton, 1985; Parton et al., 1988]; SOD2, Parton [from Parton et al., 1987]; SOD3, Fung [from Fung et al., 1987]. The base or reference case is the Mosier function, SOD1 (Figure 2).

Colorado, Temperate Arid North America. The first site a semiarid grassland region in Colorado in the western US (Figure 4a) occupied by shortgrass prairie with no woody cover. The rescaled NDVI sum representing carbon supply is only 3.4 which lies in the low end of the scale for this index, consistent with the low biomass semiarid ecosystem. The underlying soil, a luvisol Kastanozem, is a highly fertile soil conditioned by steppe climates (Table 1) and occurs here under conditions of about 350-mm annual precipitation which is exceeded by potential evapotranspiration (about 630 mm per year). The continental location results in mean monthly temperatures that vary within a few degrees of 0°C for five months of the year and rise to the low twenties in July and August, increasing the potential production of N₂O. However, in this summer period, moisture deficits control the ecosystem due to consistently low precipitation. Soil–water deficits are extreme for the entire second half of the year, resulting in reduced O₂ and H₂O (denitrification and nitrification, respectively) factors for most of the year. Organic matter decomposition (SOD) is moderate at this site although the three SOD functions vary considerably. The lowest is from the Mosier curve (SOD1 = 16) followed by 25 and 33 from SOD3 and SOD2, respectively.

The annual N₂O production for the base case is low, depressed by several factors that act serially during the year. N₂O production shuts down from November through April due to low temperatures; warm summer temperatures, dovetailing with moderate rainfall, create dry well-aerated soils. As a result, the seasonal pattern of N₂O is governed by elevated O₂ (denitrification) and H₂O (nitrification) indices in conjunction with low rates of decomposition in the spring, followed by trend reversals in these three factors in the summer.

Excluding the fertility factor (experiment 3) lowers N₂O from 17 to 12, an expected response since the luvisol Kastanozems here are associated with the maximum fertility index. Experiment 5 results in a similar decline in N₂O for similar reasons: the annually constant fertility parameter is reset to a middle value and the effect of organic matter availability is removed. As an attempt to focus on the climate effect, experiment 5 reflects observations

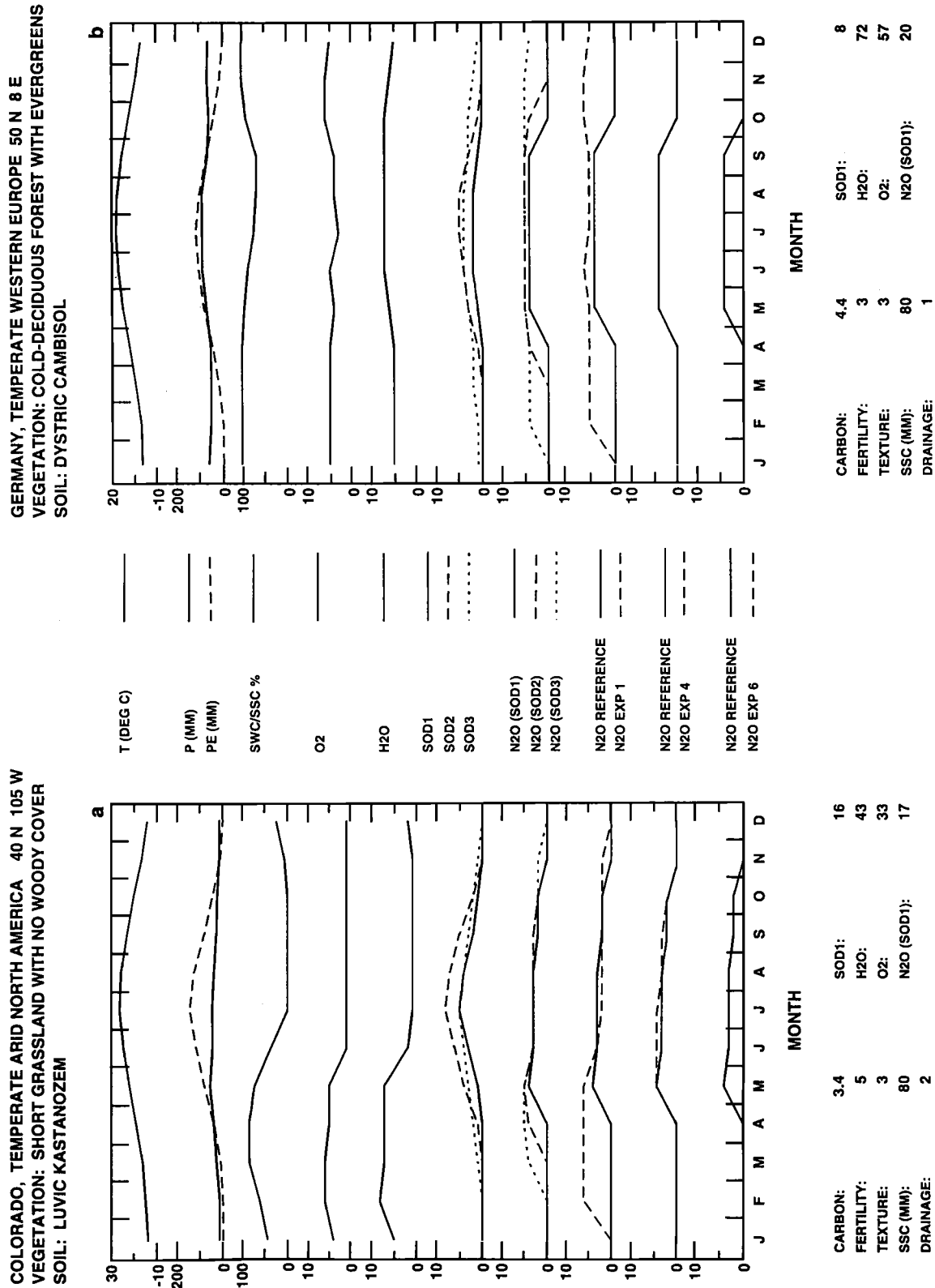


Fig. 4. Environmental characteristics, control indices, and N₂O production indices at four sites: (a) Colorado, temperate arid North America, (b) Germany, temperate western Europe, (c) Venezuela, tropical seasonal South America, and (d) Brazil, tropical humid South America. The three modeled N₂O indices are derived from the three decomposition functions shown in Fig. 2; SOD1 is used in the reference case.

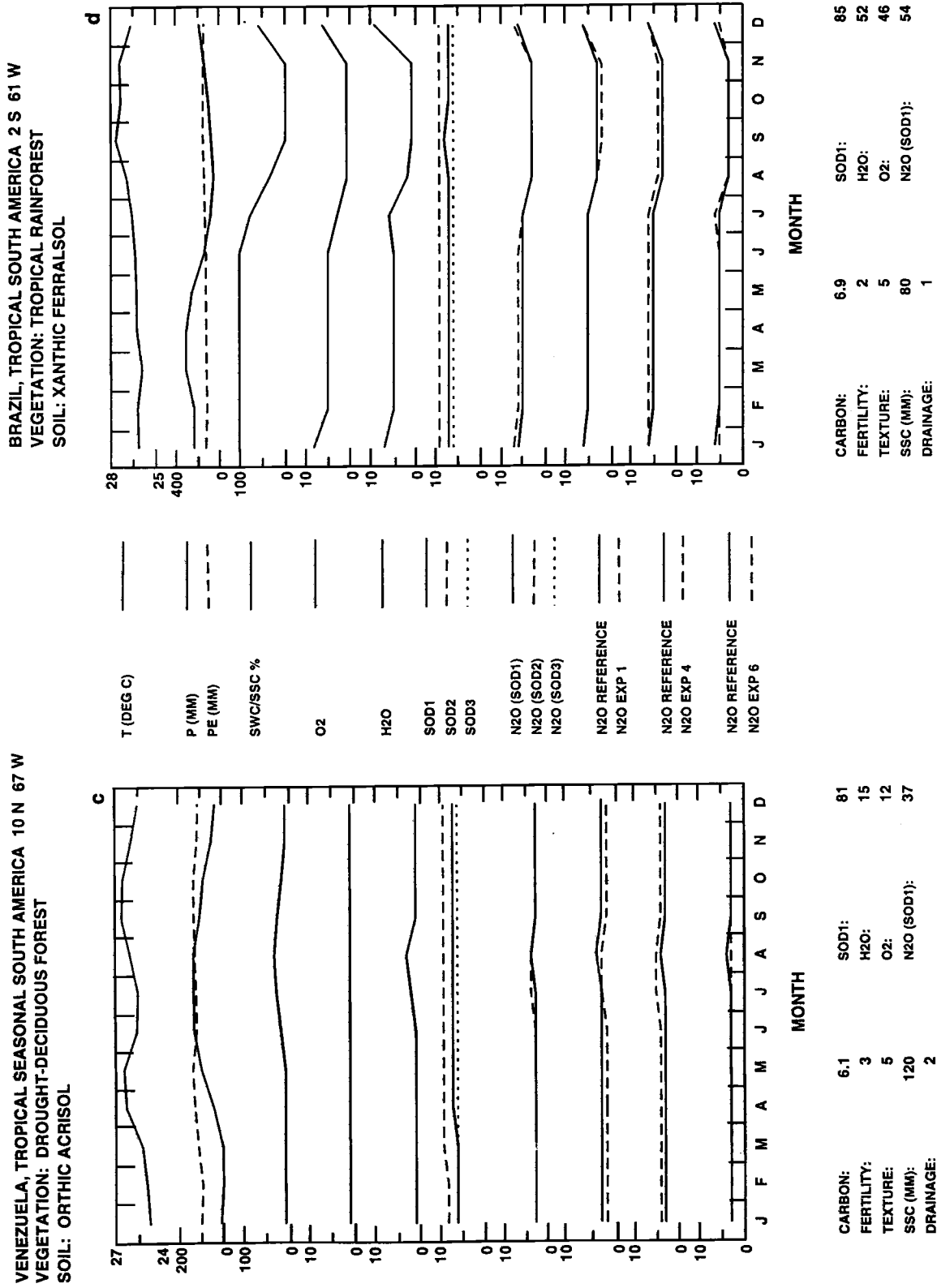


Fig. 4. (Continued).

indicating that seasonal and relatively arid temperate climates carry inherently low potential for N₂O production. Experiments 2 and 4 exhibit moderate divergence from the base case with slight increases in the annual N₂O value but little seasonal redistribution indicating that the factors evaluated in these experiments (carbon availability, oxygen limitation and soil-water history) exert approximately equal control over N₂O modeled at this site.

The highest N₂O value is for experiment 1 since seasonal temperature limitations on the decomposition of soil organic matter are relaxed in this experiment. In the reference case, monthly N₂O values are zero from November through April, and range between 4 and 2 during the productive season of May to October; in experiment 1, N₂O production rises as high as 6 and remains elevated for a long season lasting from February to November. Overall, N₂O production in this semiarid temperate environment appears to be limited by low water availability and low organic matter input.

Overall N₂O production in this semiarid temperate environment appears limited by high aerobicity, low water availability and low carbon supply which are not sufficiently counteracted by the high summer temperatures.

Germany, Temperate Western Europe. The site in western Germany is in a region of temperate deciduous forest admixed with evergreens (Figure 4b). CARBON is intermediate at 4.4; the underlying soil belongs to the dystric Cambisol group, moderately fertile soils with weak profile development, free drainage and good aeration (Table 1). The site is located in a cool wet climate characterized by a surplus of precipitation over potential evapotranspiration (820 mm and 594 mm per annum, respectively).

Organic matter decomposition at this site varies by a factor of four among the three functions; the lowest was for SOD1 (8), followed by SOD2 and SOD3 (30). SOD1 predicts low decomposition rates during a short season from May to September while SOD2 gives higher, slightly peaked, values in summer when temperatures are in the 10°–20°C range, where largest differences are expected. For the SOD3 relationship, temperature exerts weaker control on the level and duration of decomposition, resulting in relatively low and constant decomposition throughout the year. Annual N₂O estimated via the three relationships exhibits patterns similar in seasonality to their respective SOD factors and to the overall trend in temperature and H₂O; they range from the base case of 20 (SOD1) to 33 (SOD2) and 51 (SOD3). Although the predicted N₂O level is similar among the three relationships for months when they all indicate N₂O activity, the productive seasons are longer by several months with the SOD2 and SOD3 relationships.

The sensitivity experiments generally produced

minimal variations on the seasonal and total values of N₂O indicating that most parameters play equal roles in annual N₂O estimates at this site, as well as reflecting the temporally constant status of water and oxygen parameters. The only major effect, increasing N₂O to about 2.5 times that of the base case, is in experiment 1 which virtually eliminates the seasonal low-temperature limitation on decomposition and N mineralization; N₂O levels for individual months in experiment 1 are somewhat higher than those for the reference case and rise above zero for a long season extending from February through December in contrast to the five-month productive season for the base case. Since the system is well supplied with moisture throughout the year, soil-water history is not a crucial factor in the production of N₂O (experiment 6).

The results of the reference case and sensitivity experiments indicate that N₂O production in fertile, humid forest zones in moderate climates is controlled predominantly by temperature. Moisture-related parameters exert little limitation except that the relative constancy of moist soil conditions throughout the year, while contributing to conditions amenable to N₂O production, does not produce the high N₂O pulses that accompany the wetting of dry soils.

Venezuela, Tropical Seasonal South America. The South American site is occupied by drought-deciduous forest underlain by orthic Acrisols with mildly impeded drainage characteristic of wet tropical and subtropical climates with seasonal rainfall (Figure 4c). Almost half of the ~900-mm annual precipitation falls from June to August; the drier winter months (January–March) have ≤ 20 mm rainfall monthly. Constant high temperatures produce small variations in potential evapotranspiration, which ranges from 100 mm in February to 143 mm in May. This relatively flat trend in PE, combined with highly seasonal precipitation, produces conditions of moisture deficit from September to May; the season of small moisture surplus is confined to June/July and precipitation following the winter aridity produces a seasonal spike in nitrification (H₂O). As expected, the temperature-dependent decomposition functions are very similar and essentially constant through the year. Other site characteristics (fertility and drainage) are intermediate but the organic matter supply is elevated reflecting the higher deciduous biomass of the vegetation.

The reference N₂O value is less than one half the global maximum; the alternative SOD formulations are essentially equal to the reference case, i.e., highly seasonal values mimic the H₂O curve. This seasonal tropical forest site exhibits only moderate responses to the series of sensitivity experiments because of the generally neutral values of site characteristics. Although temperature is not a major controller of N₂O production in terms of seasonality,

constant high temperatures throughout the year result in rapid decomposition so that the exclusion of SOD (experiment 1) produces a decline of ~30% in modeled N₂O. For reasons mentioned above, removal of parameters seasonally constant for the site (CARBON, FERT and a combination of CARBON and soil factors) all depress the N₂O values slightly. The exclusion of the O₂ denitrification parameter (experiment 4), which mildly limits overall N₂O production here, produces the only increase in N₂O potential among the sensitivity experiments.

Under conditions of sufficient organic matter, efficiently delivered via fertile soils, the major features controlling the monthly and annual production of nitrous oxide in the tropical seasonal forest appear to be moisture conditions, reflected here in O₂ (denitrification) and H₂O (nitrification) parameters.

Brazil, Tropical South America. The Brazilian site is situated near Manaus (Figure 4d). Low fertility xanthic ferralsols are under tropical rain forest, an association common in the humid tropics. Organic matter input is high, indicated by the CARBON factor close to 7. The narrow range of annual temperatures is mirrored in the three equally constant functions describing organic matter decomposition. The reference SOD function of Mosier is intermediate at 85, while SOD2 is about 25% higher and SOD3 about 15% lower. Total precipitation is very high at about 2200 mm/year, exceeding the PE of 1675 mm/year. The constancy in temperature produces comparatively constant PE in the range of about 120–150 mm/month; although there are no very arid months, precipitation peaks at 225–300 mm/month from January to May and declines slowly to a low of 64 mm in August. Because the water storage capacity is relatively high and some precipitation continues during the dry season, the soil remains moist much of the year. More aerobic conditions in the soil are reflected in lower values of the O₂ (denitrification) and H₂O (nitrification) parameters for September through November. Increased soil aeration precedes declining anaerobicity by a month. Annual N₂O values from the three temperature functions are very similar; Mosier (SOD1) and Fung (SOD3) are both 54 while Parton (SOD2) is higher at 61, consistent with differences expected in this temperature range (Figure 2).

Experiments 1, 2 and 6 result in N₂O values slightly below the reference case. Excluding the factors accounting for organic matter input (CARBON) and decomposition (SOD), removes features that contribute to high N₂O production. Experiment 6, which evaluates the effect of the preceding month's soil water on N₂O, shows slightly lower values only for the first half of the year. The remaining experiments all increase N₂O estimates in this tropical site, by larger values than the declines

of the other experiments: removal of the (low) fertility factor increases the annual total by about 12%; the same increase is produced in experiment 5 in which the low fertility of 2 is prescribed at 3 and the CARBON factor is excluded. The largest response, an increase of ~20%, comes from experiment 4 in which the role of denitrification was excluded. Although this location has considerable organic matter turnover, it has low fertility well-drained soils characteristic of tropical forest regions. Furthermore, the high annual precipitation is sufficiently seasonal to reduce considerably N₂O production capability for about half the year.

4.4 Comparison With Field Measurements

Modeled monthly N₂O is compared with measured N₂O fluxes in various natural ecosystems (Table 8). This comparison allows a general evaluation of the model and data bases in a variety of environments, as well as providing a framework for translating nondimensional N₂O values into N₂O fluxes.

Several observations are excluded from the comparison because site descriptions are incomplete, or the climate, soil conditions or vegetation types from the 1° data bases corresponding to measurement locations differ from those reported. In some cases, the mean of N₂O values of a surrounding pair of cells with conditions essentially identical to the measurement site is compared to the measured flux.

The reference case using the SOD1 function (Figure 5) yields the best fit to the measured fluxes (r^2 for least squares fit to a quadratic function = 0.55). SOD2 and SOD3 (not shown) result in r^2 of 0.38 and 0.24, respectively. The r^2 for quadratic fits are 0.16, 0.48, 0.55, 0.43, 0.42, 0.60, and 0.33 for experiments 1–7, respectively.

Relative to the reference case, exclusion of the temperature effect (experiment 1) causes a large reduction in r^2 from 0.55 to 0.16, a dramatic increase in N₂O in temperate sites (particularly in temperate climates during autumn, winter and spring), and a moderate decline in N₂O values for tropical sites. In temperate summers with sufficient soil moisture, however, temperatures may be comparable with or even higher than those in the tropics. Hence, the effect of excluding SOD in summer is less important than in temperate winters.

As shown in section 4.2, the factor CARBON provides additional variability within climatic and soil regions. However, for the measurement sites considered, the exclusion of CARBON (experiment 2) reduces r^2 from 0.55 in the reference case to 0.48. Using only CARBON to predict N₂O production (experiment 7) gives r^2 of 0.33 and a large increase in N₂O particularly in temperate ecosystems.

Although soil fertility may be the principal cause of variation in N₂O fluxes regionally, exclusion of soil-fertility variations globally (experiment 3) has

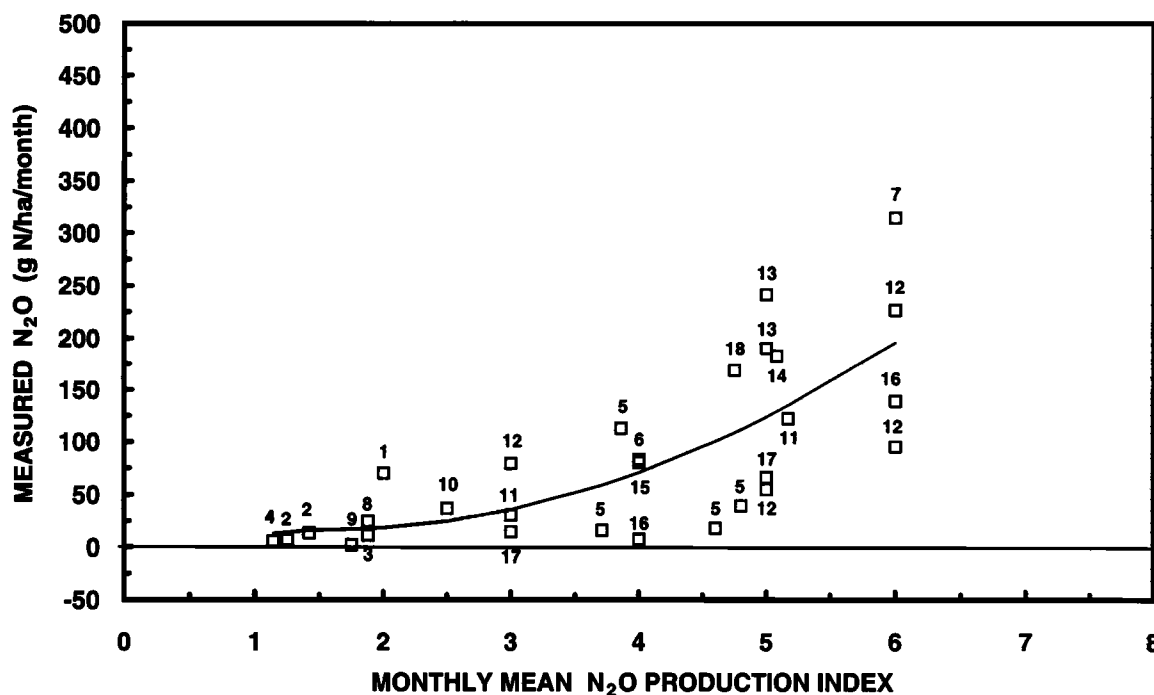


Fig. 5. Relationship between measured N₂O fluxes and modeled N₂O from the reference case for a series of field sites. Labels refer to sites listed in Table 8. The solid line represents the best quadratic fit: for N₂O > 1.5, flux = $9.01 \times (\text{N}_2\text{O})^2 - 27.87 \times (\text{N}_2\text{O}) + 38.22$; for N₂O ≤ 1.5, flux = $11.13 \times (\text{N}_2\text{O})$.

no major effect on the comparison except at temperate sites with high soil fertility (e.g., sites 1 and 2 in Figure 5). Experiment 3 suggests that the soil fertility scale used here does not resolve sufficiently the fertility variations found in natural conditions.

Excluding the oxygen limitation of soils (experiment 4) results in a value for r^2 of 0.43. Globally uniform soil texture, drainage and fertility (experiment 5) reduces r^2 from 0.55 to 0.42, suggesting that variations in these controls capture important information on N₂O flux variations on a global scale. Exclusion of the factor O₂ (experiment 4) overpredicts N₂O production in well drained soils.

Experiment 6 considers the status of soil water and oxygen of the current month only, and results in an r^2 of 0.60. The change is mainly caused by a decrease in N₂O in December for one site near Manaus, Brazil (Table 8, site 12) [Keller et al., 1986]. This and minor shifts for some other points causes a slightly improved correlation. The r^2 for the reference case and experiment 6 are similar, but since the major difference is a shift of only one point, the reference case was maintained.

4.5 Estimate of the Global Preagricultural N₂O Emission

A regression relationship is obtained between measured N₂O fluxes and modeled (reference case) N₂O production indices (N₂O). This relationship is applied to the global distributions of monthly N₂O

indices to estimate monthly fluxes. The global emission thus calculated is 6.8 Tg N₂O-N y⁻¹. The tropics (± 30° of the equator) contribute 5.4 Tg N₂O-N y⁻¹ and the emission from extra-tropical regions (poleward of 30°) is 1.4 Tg N₂O-N y⁻¹.

The role of the world's wetlands in the nitrous oxide budget is uncertain. For tropical and temperate wetlands, partially represented by organic soils (group 23), the model may overestimate the potential for N₂O production. In these wetlands anaerobicity resulting from high water tables may block nitrification; this may limit denitrification rates. Furthermore, under very wet conditions, nitrous oxide can be consumed to serve as an electron acceptor. Therefore, wetlands could act as a sink for N₂O during part(s) of the year. One problem is that many wetlands mapped by Matthews and Fung [1987], ~525 × 10⁶ ha globally, do not coincide with the organic soils identified in the soils data base used here. We repeated the above calculation excluding areas designated as wetlands by Matthews and Fung [1987]. In this calculation, emission and consumption of N₂O in wetlands are assumed to be equal. Wetlands cover only about 4% of the ice-free land area, and their exclusion from the analysis causes a decline in the modeled global N₂O emission of a few percent. We do not know whether N₂O emission from tropical wetlands is overestimated here, but the analysis suggests that the global contribution of wetlands to the N₂O budget is minor.

5. CONCLUSIONS

The model results show that spatial and seasonal distributions of N₂O production are very similar to climate patterns. Low winter temperatures limit N₂O production in temperate regions while in the tropics, temperature does not limit the processes involved in N₂O production. In the wet tropics, where organic matter inputs are high and both soil moisture conditions and temperatures are favorable, N₂O indices (N₂O) are among the highest. This is consistent with high emissions reported for tropical forests (Table 8). While it is tempting to conclude that climate is the most important control factor, we note that C/N ratios and lignin content of the litter are not included explicitly as controls in the model. However, as their geographic variations mirror, to some extent, those of climate, we conclude that the pattern of N₂O production is determined, to first order, by the pattern of climate variation. Together with physical soil conditions, climate determines oxygen limitation and water availability. The factors FERT and O₂ introduce variability among sites, without producing major impacts on the level of the N₂O values.

The lack of major differences in predicted N₂O between the reference case and experiment 3, in which the role of soil fertility is investigated, suggests that the model does not adequately reflect fertility levels among soils. In practice, only broad properties for soil groups are used and information to distinguish fertility differences among soil types within groups is lacking. Exclusion of the fertility index increases the variability of the N₂O potential, reflecting the simplicity of the scale.

The variability in N₂O production (expressed as the percentage of the standard deviation of the N₂O index relative to the mean within each soil group) is highest in ecosystems with overall low N₂O values, i.e., in moist temperate climates, and in both temperate and tropical environments under arid and semiarid regimes. Apparently, where climate (soil water and/or temperature) is most limiting, variability in other factors results in higher percent standard deviations than those in regions with climatic conditions favorable for N₂O production; absolute standard deviations are highest in areas with high N₂O production potential.

Comparison with measurement data shows that predicted levels of N₂O production are in general agreement with measured fluxes, even though responses to long-term mean climate are compared with responses to local weather conditions prevailing during measurement periods. The ~30 flux measurements used for the comparison represent only six different ecosystems (wetlands, temperate forests, steppe, tropical savannas, tropical dry forests, and tropical rain forest). It is difficult to draw conclusions about the relative importance of various parameters on the basis of this limited data set. In addition, it is difficult to assess published

measurements of nitrous oxide fluxes. In many measurement reports, site descriptions are incomplete: climate data are often absent, or provided only as annual mean precipitation and temperature; imprecise descriptions of conditions during the period of measurements are common; complete descriptions of chemical and physical soil characteristics, such as pH, texture, structure, drainage condition and soil classification, are rarely reported.

Because of the simplicity of the model and the sparsity of data, the estimate of global N₂O emission from natural ecosystems based on the regression analysis is extremely uncertain. To improve models of this type, more measurements are needed in those places expected to have high N₂O fluxes, and in regions or ecosystems which may be important contributors to the global production of N₂O due to their large area. Globally, only about 30 measurements have complete enough information to allow comparison; these do not include any data for Asia, Africa or Australia. We do not know how well the model performs in these areas with different environmental conditions and soils.

The role of soil sinks needs to be addressed in future. Consumption of N₂O has been reported [e.g., Ryden, 1981, 1983]. If this is a common phenomenon, it may have important implications for the N₂O global budget [Cicerone, 1989]. Data on consumption are too scarce to describe this process in a global model such as this one.

The 1° resolution of the soil data base does not reflect the detail of the 1:5 M soil map [FAO/Unesco, 1974-1981] used in its compilation. In digitizing the soil map, only the dominant soil type was recorded [Zobler, 1986] so that many of the associated or included soils are not represented. These minor soils may be of importance for trace gas emissions. In particular, wetlands and hydromorphic soils are poorly represented because they occur frequently as linear and scattered features that do not dominate at the 1° resolution. Even at the 1:5M scale of the FAO/Unesco soil map, they are under-represented [Van Diepen, 1985]. Parallel to the need for greater spatial resolution is the need for greater information resolution about soil fertility, drainage, and texture. In the model, only five levels of these properties are resolved, although there are >100 soil types. To improve the model, soil data bases including a number of soil characteristics vital to evaluating fertility are required. More spatial and temporal detail in data bases of vegetation (NPP) and litter composition would allow a better description of the temporal and geographic variability of controls on N₂O fluxes and, possibly, episodic pulses of N₂O.

The latitudinal and seasonal distributions of N₂O fluxes modeled here may be used as inputs to two- and three-dimensional models of the atmosphere to test hypotheses about the N₂O budget.

APPENDIX A

The primary gridded data sets used in the model, commented upon briefly in the text, are discussed more fully below.

A.1. *Climate*

Shea [1986] produced climatologies of monthly surface air temperature and precipitation, at 2.5° resolution for the globe, from station observations. Lacking a global climatology for soil temperatures, we used surface air temperatures. This may introduce phase errors, of up to a season in middle and high latitudes, in the seasonality of N₂O production.

A.2. *Soil Type, Texture, Fertility, and Drainage*

The global distribution of soil properties was obtained from the data base of Zobler [1986], compiled in digital form at 1° resolution from the FAO/Unesco [1974–1981] Soil Map of the World. The 1:5M FAO/Unesco soil maps distinguish dominant soil units, associated soils and inclusions, topsoil texture of the dominant soil and slope. On the maps, additional information on phases is indicated with special symbols. The full digital data base of Zobler [1986] includes distributions of major and associated soil units, soil texture, slope, and phase. The data sets used in this study are major soil units and soil texture.

The FAO/Unesco [1974–1981] soil classification system has two levels: soil groups and soil units. There are 26 soil groups encompassing 106 soil units. The soil groups and soil units are classified on the basis of diagnostic horizons and diagnostic properties. Descriptions of the soil groups and soil units can be found in the works by FAO/Unesco [1974–1981], Fitzpatrick [1983] and Driessen and Dudal [1991]. Two of the soil units, gelic Planosols, and ferric Podzols, do not occur in the digital data base because they never dominate at 1° resolution.

For this study, soil units are aggregated into 23 new groups. Table 1 lists the 23 groups and their areas, presented under 10 higher-level soil clusters (I–X). The global distribution of the 23 new groups is shown in Plate 1. Soils are formed through the impact of climate, vegetation, fauna (including humans) and topography on the parent material. The relative influence of these soil-forming factors varies among sites, explaining the considerable variety found in soils. Globally, climate is the major soil-forming factor and under similar climatic conditions, soil development is sufficiently consistent to form a basis for soil classification. Such zonal soils are represented in Table 1 by clusters II–IV and VI–VII. Variations occur where parent rock (clusters VIII and X), physiographic position (IX) or other local features dominate soil

formation. These soils are intrazonal and azonal soils with no clear relation to vegetation and climate.

In this model, individual gelic soil types are combined to form the permafrost soil cluster. In addition, several soils are combined following the new terminology of FAO/Unesco [1988]: all shallow soils (Lithosols, Rankers, and Rendzinas) are grouped as Leptosols (group 21), and weakly-developed soils under arid and semiarid moisture regimes, Xerosols and Yermosols, are grouped as desert soils (group 14).

The data base of soil units provides the basis for deriving information on two factors in the model: fertility and drainage. Indices for these factors, ranging from one to five, are associated with each of the 106 soil units as shown in Table 1 and discussed in section 3.

The reliability of the FAO/Unesco soil map is not spatially uniform. Reliability is particularly low in the Amazon basin, the former Soviet Union, parts of eastern Africa, and Europe. Additional information has become available since compilation of the FAO/Unesco soil maps in the 1960s, reflected in the revised legend of FAO/Unesco [1988].

Topsoil texture is defined as the relative proportions of clay (particles < 2 μm), silt (2–50 μm), and sand (50–2000 μm) in the top 30 cm of the soil. The FAO/Unesco soil maps have three broad texture classes for the topsoil: coarse, medium, and fine. In addition to these texture classes, the digital data set identifies several texture combinations; the organic class is for nonmineral topsoils (Table 2). Topsoils with coarse textures have <18% clay and >65% sand and include sands, loamy sands and sandy loams. The medium texture class, with <35% clay and <65% sand, includes sandy loams, loams, sandy clay loams, silt loams, silt s, silty clay loams, and clay loams. Fine-textured topsoils have >35% clay and include clays, silty clays, sandy clays, clay loams, and silty clay loams. The reader is referred to the texture triangle in FAO/Unesco [1974–1981] and to U.S. Department of Agriculture [1975] for further information on characteristics of texture classes.

A.3. *Vegetation*

The satellite-derived normalized difference vegetation index (NDVI) is a measure of the primary productivity of vegetation [Box et al., 1989]. The NDVI is calculated as the difference between radiances in the visible (0.58–0.68 μm) and near infrared (0.725–1.1 μm) portions of the spectrum normalized by the sum of the radiances. The Advanced Very High Resolution Radiometer (AVHRR) on board the NOAA series of polar-orbiting satellites [Tarpley et al., 1984] routinely measures the radiances. The weekly maximum NDVI's at ~25 km resolution obtained from NOAA for 1984 were further sampled and averaged for this study. First, the maximum monthly NDVI at 25 km

resolution was retained from the weekly maxima. These dates were then averaged to 1° resolution. The digital data base of vegetation types compiled by Matthews [1983] is used for verifying measurement site characteristics and for analysis of model results.

Acknowledgments. NASA Biogeochemistry and Geophysics Branch provided funding for this project. Three anonymous reviewers provided extensive comments that led to improvement in the paper. We gratefully acknowledge the technical assistance of Lilly Del Valle and Christina Koizumi.

REFERENCES

- Adams, S. N., W. H. Jack, and D. A. Dickson, The growth of Sitka spruce on poorly drained sites in northern Ireland, *Forestry*, 43, 125-133, 1970.
- Alexander, M., *Introduction to Soil Microbiology*, 2nd ed., 467 pp., John Wiley, New York, 1977.
- Anderson, I. C., J. S. Levine, M. A. Poth, and P. J. Riggan, Enhanced biogenic emissions of nitric oxide and nitrous oxide following surface biomass burning, *J. Geophys. Res.*, 93, 3893-3898, 1988.
- Anderson, I. C., and M. A. Poth, Semiannual losses of nitrogen as NO and N₂O from unburned and burned chaparral, *Global Biogeochem. Cycles*, 3, 121-135, 1989.
- Anderson, J. M., Responses of soils to climate change, *Adv. Ecol. Res.*, 22, 163-210, 1992.
- Banin, A., Global budget of N₂O: The role of soils and their change, *Sci. Total Environ.*, 55, 27-38, 1986.
- Blackmer, A. M., J. M. Bremner, and E. L. Schmidt, Production of N₂O by ammonium oxidizing chemoautotrophic microorganisms in soil, *Appl. Environ. Microbiol.*, 40, 1060-1066, 1980.
- Blackmer, A. M., S. G. Robbins, and J. M. Bremner, Diurnal variability in rate of emission of nitrous oxide from soils, *Soil Sci. Soc. Am. J.*, 46, 937-942, 1982.
- Blokhus, W. A., Vertisols, in *Lecture notes on the geography, formation properties and use of the major soils of the world*, edited by P. M. Driessen and R. Dudal, pp. 77-91, Agricultural University, Wageningen and Katholieke Universiteit, Leuven, 1991.
- Boring, L. R., W. T. Swank, J. B. Waide, and G. S. Henderson, Sources, fates and impacts of nitrogen inputs to terrestrial ecosystems: Review and synthesis, *Biogeochemistry*, 6, 119-159, 1988.
- Bowden, R. D., P. A. Steudler, J. M. Melillo, and J. D. Aber, Annual nitrous oxide fluxes from temperate forest soils in the northeastern United States, *J. Geophys. Res.*, 95, 13,997-14,005, 1990.
- Bowden, W. B., Gaseous nitrogen emissions from undisturbed terrestrial ecosystems: An assessment of their impacts on local and global nitrogen budgets, *Biogeochemistry*, 2, 249-279, 1986.
- Box, E. O., B. N. Holben, and V. Kalb, Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO₂ flux, *Vegetatio*, 80, 71-89, 1989.
- Brady, N. C., *The Nature and Properties of Soils*, 8th ed., 639 pp., Macmillan, New York, 1976.
- Breitenbeck, G. A., A. M. Blackmer, and J. M. Bremner, Effects of different nitrogen fertilizers on emission of nitrous oxide from soil, *Geophys. Res. Lett.*, 7, 85-88, 1980.
- Bremner, J. M., and A. M. Blackmer, Terrestrial nitrification as a source of atmospheric nitrous oxide, in *Denitrification, Nitrification and Atmospheric Nitrous Oxide*, edited by C. C. Delwiche, pp. 151-170, John Wiley, New York, 1981.
- Bremner, J. M., S. G. Robbins, and A. M. Blackmer, Seasonal variability in emission of nitrous oxide from soil, *Geophys. Res. Lett.*, 7, 641-644, 1980.
- Brumme, R., and F. Beese, Effects of liming and nitrogen fertilization on emissions of CO₂ and N₂O from a temperate forest, *J. Geophys. Res.*, 97, 12,851-12,851, 1992.
- Cates, R. L., and D. R. Keeney, Nitrous oxide emission from native and reestablished prairies in southern Wisconsin, *Am. Midland Nat.*, 117, 35-42, 1987.
- Christensen, S., and J. M. Tiedje, Brief and vigorous N₂O production by soil at spring thaw, *J. Soil Sci.*, 41, 1-4, 1990.
- Cicerone, R., Analysis of sources and sinks of atmospheric nitrous oxide (N₂O), *J. Geophys. Res.*, 94, 18,265-18,271, 1989.
- Colbourn, P., and I. W. Harper, Denitrification in drained and undrained arable clay soil, *J. Soil Sci.*, 38, 531-539, 1987.
- Colbourn, P., I. W. Harper, and M. M. Iqbal, Denitrification losses from ¹⁵N labelled calcium fertilizer in a clay soil in the field, *J. Soil Sci.*, 35, 539-547, 1984.
- Crutzen, P. J., The influence of nitrogen oxides on the atmospheric ozone content, *Q. J. R. Meteorol. Soc.*, 96, 320-325, 1976.
- Davidson, E. A., Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems, in *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides and Halomethanes*, edited by J. E. Rogers and W. B. Whitman, pp. 219-235, American Society for Microbiology, Washington, D.C., 1991.
- Denmead, O. T., J. R. Freney, and J. R. Simpson, Studies of nitrous oxide emission from a grass sward, *Soil Sci. Soc. Am. J.*, 43, 726-728, 1979.
- Dickinson, R. E., A. Henderson-Sellers, P. J. Kennedy, and M. F. Wilson, Biosphere/Atmosphere Transfer Scheme (BATS) for the NCAR Community Climate Model, *NCAR Tech. Note TN-275*, Nat. Cent. for Atmos. Res., Boulder, Colo., 1986.
- Dijkerman, J. C., Ferralsols, in *Lecture Notes on the*

- Geography, Formation Properties and Use of the Major Soils of the World*, edited by P. M. Driessen and R. Dudal, pp. 159-169, Agricultural University, Wageningen and Katholieke Universiteit, Leuven, 1991.
- Dowdell, R. J., and K. A. Smith, Field studies of the soil atmosphere, II. Occurrence of nitrous oxide, *J. Soil Sci.*, 25, 231-238, 1974.
- Driessen, P. M., and R. Dudal, *Lecture Notes on the Geography: Formation, Properties and Use of the Major Soils of the World*, 296 pp., Agricultural University Wageningen, Katholieke Universiteit Leuven, 1991.
- Duxbury, J. M., D. R. Bouldin, R. E. Terry, and R. L. Tate III, Emissions of nitrous oxide from soils, *Nature*, 298, 462-464, 1982.
- Duxbury, J. M., M. S. Smith, J. W. Doran, C. Jordan, L. Szott, and E. Vance, Soil organic matter as a source and a sink of plant nutrients, in *Dynamics of Soil Organic Matter in Tropical Ecosystems*, edited by D. C. Coleman, J. M. Oades, and G. Uehara, pp. 33-67, NifTAL Project, Department of Agronomy and Soil Science, College of Tropical Agriculture and Human Resources, University of Hawaii, 1989.
- Eaton, L. J., and D. G. Patriquin, Denitrification in lowbush blueberry soils, *Can. J. Soil Sci.*, 69, 303-312, 1989.
- Elkins, J. W., T. M. Thompson, B. D. Hall, K. B. Egan, and J. H. Butler, NOAA/GMCC halocarbons and nitrous oxide measurements at the South Pole, *Antarctic. J.*, 23, 176-177, 1988.
- Euroconsult, *Agricultural Compendium for Rural Development in the Tropics and Subtropics*, 740 pp., Elsevier, New York, 1989.
- Firestone, M. K., and E. A. Davidson, Microbiological basis of NO and N₂O production and consumption in soil, in *Exchange of Trace Gases Between Terrestrial Ecosystems and the Atmosphere*, edited by M. O. Andreae and D. S. Schimel, pp. 7-21, John Wiley, New York, 1989.
- Firestone, M. K., R. B. Firestone, and J. M. Tiedje, Nitrous oxide from soil denitrification: Factors controlling its biological production, *Science*, 208, 749-751, 1980.
- Fitzpatrick, E. A., *Soils. Their Formation, Classification and Distribution*, 355 pp., Longman, London New York, 1983.
- Focht, D. D., The effect of temperature, pH and aeration on the production of nitrous oxide and gaseous nitrogen - a zero order kinetic model, *Soil Sci.*, 118, 173-179, 1974.
- Folorunso, O. A., and D. E. Rolston, Spatial variability of field measured denitrification gas fluxes, *Soil Sci. Soc. Am. J.*, 48, 1214-1219, 1984.
- Food and Agriculture Organization (FAO), Methodology and Results for South and Central America, in *Rep. Agro-Ecol. Zones Proj.*, 3, 251 pp., FAO, Rome, 1981.
- Food and Agriculture Organization (FAO)/Unesco, *Soil Map of the World*, pp., 1:5,000,000, vol. I-X, Unesco, Paris, 1974-1981.
- Food and Agriculture Organization (FAO)/Unesco, *Soil Map of the World, Revised Legend*, World Resources Rep. 60, FAO, Rome, 1988.
- Fung, I. Y., C. J. Tucker, and K. C. Prentice, Application of advanced very high resolution radiometer vegetation index to study atmosphere-biosphere exchange of CO₂, *J. Geophys. Res.*, 92, 2999-3015, 1987.
- Goodroad, L. L., and D. R. Keeney, Nitrous oxide emission from forest, marsh and prairie ecosystems, *J. Environ. Qual.*, 13, 448-452, 1984a.
- Goodroad, L. L., and D. R. Keeney, Nitrous oxide production in aerobic soils under varying pH, temperature and water content, *Soil Biol. Biochem.*, 16, 39-43, 1984b.
- Goodroad, L. L., and D. R. Keeney, Site of nitrous oxide production in field soils, *Biol. Fert. Soils*, 1, 3-7, 1985.
- Gordon, A. S., W. J. Cooper, and D. J. Scheidt, Denitrification in marl and peat sediments in the Florida Everglades, *Appl. Environ. Microbiol.*, 52, 987-991, 1986.
- Goward, S. N., C. J. Tucker, and D. G. Dye, North American vegetation patterns observed with the NOAA-7 advanced very high resolution radiometer, *Vegetatio*, 64, 3-14, 1986.
- Greaves, J. E., and E. G. Carter, Influence of soil moisture on the bacterial activities of the soil, *Soil Sci.*, 10, 361-387, 1920.
- Groffman, P. M., and J. M. Tiedje, Denitrification hysteresis during wetting and drying cycles in soil, *Soil Sci. Soc. Am. J.*, 52, 1626-1629, 1988.
- Groffman, P. M., and J. M. Tiedje, Denitrification in North temperate forest soils: Spatial and temporal patterns at the landscape and seasonal scales, *Soil Biol. Biochem.*, 21, 613-620, 1989.
- Hao, W. M., D. Scharffe, P. J. Crutzen, and E. Sanhueza, Production of N₂O, CH₄, and CO₂ from soils in the tropical savanna during the dry season, *J. Atmos. Chem.*, 7, 93-105, 1988.
- Hao, W. M., S. C. Wofsy, M. B. McElroy, J. M. Beer, and M. A. Toqan, Sources of atmospheric nitrous oxide from combustion, *J. Geophys. Res.*, 92, 3098-3104, 1987.
- Hillel, D., *Applications of Soil Physics*, 385 pp., Academic, San Diego, Calif., 1980.
- Isaksen, I. S. A., V. Ramaswamy, H. Rodhe, and T. M. L. Wigley, Radiative forcing to climate, in *Climate Change 1992. The Supplementary Report to the IPCC Scientific Assessment*, edited by J. T. Houghton, B. A. Callander and S. K. Varney, pp. 49-67, Cambridge University Press, New York, 1992.
- Jenkinson, D. S., and A. Ayanaba, Decomposition of carbon-14 labeled plant material under tropical conditions, *Soil Sci. Soc. Am. J.*, 41, 912-915, 1977.
- Jordan, C. F., *Nutrient Cycling in Tropical Forest*

- Ecosystems: Principles and Their Application in Management and Conservation*, 179 pp., John Wiley, New York, 1985.
- Keeney, D. R., I. R. Fillery, and G. P. Marx, Effect of temperature on gaseous nitrogen products of denitrification in a silt loam soil, *Soil Sci. Soc. Am. J.*, 43, 1124-1128, 1979.
- Keller, M., T. J. Goreau, S. C. Wofsy, W. A. Kaplan, and M. B. McElroy, Production of nitrous oxide and consumption of methane by forest soils, *Geophys. Res. Lett.*, 10, 1156-1159, 1983.
- Keller, M., W. A. Kaplan, and S. C. Wofsy, Emissions of N₂O, CH₄, and CO₂ from tropical forest soils, *J. Geophys. Res.*, 91, 11,791-11,802, 1986.
- Keller, M., W. A. Kaplan, S. C. Wofsy, and J. M. DaCosta, Emission of N₂O from tropical soils: Response to fertilization with NH₄⁺, NO₃⁻, and PO₄³⁻, *J. Geophys. Res.*, 93, 1600-1604, 1988.
- Khalil, M. A. K., and R. A. Rasmussen, The global sources of nitrous oxide, *J. Geophys. Res.*, 97, 14,651-14,660, 1992.
- Klemetsson, L., B. H. Svensson, and T. Rosswall, Relationships between soil moisture content and nitrous oxide production during nitrification and denitrification, *Biol. Fert. Soils*, 6, 106-111, 1988.
- Landon, J. R., *Booker Tropical Soil Manual. A Handbook For Soil Survey and Agricultural Land Evaluation in the Tropics and Subtropics*, Booker Agriculture International Limited, Longman, New York, 1984.
- Letey, J., N. Valoras, D. D. Focht, and J. C. Ryden, Nitrous oxide production and reduction during denitrification as affected by redox potential, *Soil Sci. Soc. Am. J.*, 45, 727-730, 1981.
- Li, C., S. Frolking, and T. A. Frolking, A model of nitrous oxide evolution from soil driven by rainfall events: 1. Model structure and sensitivity, *J. Geophys. Res.*, 97, 9759-9776, 1992.
- Linn, D. M., and J. W. Doran, Effect of water filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils, *Soil Sci. Soc. Am. J.*, 48, 1267-1272, 1984.
- Lipschultz, F., O. C. Zafiriou, S. C. Wofsy, M. B. McElroy, F. W. Valois, and S. W. Watson, Production of NO and N₂O by soil nitrifying bacteria, *Nature*, 294, 641-643, 1981.
- Livingston, G. P., P. M. Vitousek, and P. A. Matson, Nitrous oxide flux and nitrogen transformations across a landscape gradient in Amazonia, *J. Geophys. Res.*, 93, 1593-1599, 1988.
- Luizao, F., P. Matson, G. Livingston, R. Luizao, and P. Vitousek, Nitrous oxide flux following tropical land clearing, *Global Biogeochem. Cycles*, 3, 281-285, 1989.
- Manabe, S., Climate and ocean circulation, Part I: The atmospheric radiation and the hydrology of the Earth's surface, *Mon. Weather Rev.*, 93, 739-774, 1969.
- Martikainen, P. J., Nitrous oxide emission associated with autotrophic ammonium oxidation in acid coniferous forest soil, *Appl. Environ. Microbiol.*, 50, 1519-1525, 1985.
- Matson, P. A., and P. M. Vitousek, Cross-ecosystem comparisons of soil nitrogen and nitrous oxide flux in tropical ecosystems, *Global Biogeochem. Cycles*, 1, 163-170, 1987.
- Matson, P. A., and P. M. Vitousek, Ecosystem approach for the development of a global nitrous oxide budget, *Bioscience*, 40, 667-672, 1990.
- Matson, P. A., P. M. Vitousek, and D.S. Schimel, Regional extrapolation of trace gas flux based on soils and ecosystems, in *Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere*, edited by M.O. Andreae and D.S. Schimel, pp. 97-108, Dahlem Workshop Report, John Wiley, New York, 1989.
- Matson, P. A., P. M. Vitousek, G. P. Livingston, and N. A. Swanberg, Sources of variation in nitrous oxide flux from Amazonian ecosystems, *J. Geophys. Res.*, 95, 16,780-16,798, 1990.
- Matthews, E., Global vegetation and land use: New high resolution data bases for climate studies, *J. Clim. Appl. Meteorol.*, 22, 474-487, 1983.
- Matthews, E., and I. Fung, Methane emission from natural wetlands: Global distribution, area, and environmental characteristics of sources, *Global Biogeochem. Cycles*, 1, 61-86, 1987.
- Miller, H. G., Forest fertilization: Some guiding concepts, *Forestry*, 54, 157-167, 1981.
- Mintz, Y., and Y. Serafini, Global fields of soil moisture and land surface evapotranspiration, *Tech. Memo. 83907*, Res. Rev. 1980/81, pp. 178-180, NASA Goddard Space Flight Cent., Greenbelt, Md., 1981.
- Mosier, A. R., W. D. Guenzi, and E. E. Schweizer, Soil losses of dinitrogen and nitrous oxide from irrigated crops in Northeastern Colorado, *Soil Sci. Soc. Am. J.*, 50, 344-348, 1986.
- Mosier, A. R., and W. J. Parton, Denitrification in a shortgrass prairie: A modelling approach, in *Planetary Ecology*, edited by D. E. Caldwell, J. A. Brierley and C. L. Brierley, pp. 441-451, Van Nostrand Reinhold, New York, 1985.
- Mosier, A. R., M. Stillwell, W. J. Parton, and R. G. Woodmansee, Nitrous oxide emissions from a native shortgrass prairie, *Soil Sci. Soc. Am. J.*, 45, 617-619, 1981.
- Mulvaney, R. L., and L. T. Kurtz, Evolution of dinitrogen and nitrous oxide from nitrogen-15 fertilized soil cores subjected to wetting and drying cycles, *Soil Sci. Soc. Am. J.*, 48, 596-602, 1984.
- Muzio, L. J., and J. C. Kramlich, An artifact in the measurement of N₂O from combustion sources, *Geophys. Res. Lett.*, 15, 1369-1373, 1988.
- Myrold, D. D., and J. M. Tiedje, Diffusional constraints on denitrification in soil, *Soil Sci. Soc. Am. J.*, 49, 651-657, 1985.
- Nye, P. H., and P. B. Tinker, *Solute Movements in*

- the Soil-Root System*, 342 pp., Blackwell, Oxford, 1977.
- Oades, J. M., The retention of organic matter in soils, *Biogeochemistry*, 5, 35-70, 1988.
- Ottow, J. G. G., I. Burth-Gebauer, and M. E. E. Demerdash, Influence of pH and partial oxygen pressure on the N₂O-N to N₂ ratio of denitrification, in *Denitrification in the Nitrogen Cycle*, edited by H. L. Golterman, pp. 101-120, Plenum, New York, 1985.
- Parkin, T. B., Soil microsites as a source of denitrification variability, *Soil Sci. Soc. Am. J.*, 51, 1194-1199, 1987.
- Parkin, T. B., A. J. Sextone, and J. M. Tiedje, Adaptation of denitrifying populations to low soil pH, *Appl. Environ. Microbiol.*, 49, 1053-1056, 1985.
- Parton, W. J., A. R. Mosier, and D. S. Schimel, Rates and pathways of nitrous oxide production in a shortgrass steppe, *Biogeochemistry*, 6, 45-48, 1988.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima, Analysis of factors controlling soil organic matter levels in Great Plains grasslands, *Soil Sci. Soc. Am. J.*, 51, 1173-1179, 1987.
- Post, W. M., J. Pastor, P. J. Zinke, and A. G. Stangenberger, Global patterns of soil nitrogen storage, *Nature*, 317, 613-616, 1985.
- Poth, M., and D. D. Focht, ¹⁵N kinetic analysis of N₂O production by *Nitrosomonas europaea*: An examination of nitrifier denitrification, *Appl. Environ. Microbiol.*, 49, 1134-1141, 1985.
- Prinn, R., D. Cunnold, R. Rasmussen, P. Simmonds, F. Alyea, A. Crawford, P. Fraser, and R. Rosen, Atmospheric emissions and trends of nitrous oxide deduced from ten years of ALE-GAGE data, *J. Geophys. Res.*, 95, 18,369-18,385, 1990.
- Robertson, G. P., Nitrification and denitrification in humid tropical ecosystems: Potential controls on nitrogen retention, in *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*, edited by J. Proctor, pp. 55-69, Blackwell Scientific Publications, Oxford, 1989.
- Robertson, G. P., and J. M. Tiedje, Denitrification and nitrous oxide production in successional and old-growth Michigan forests, *Soil Sci. Soc. Am. J.*, 48, 383-389, 1984.
- Robertson, G. P., and J. M. Tiedje, Nitrous oxide sources in aerobic soils: Nitrification, denitrification and other biological processes, *Soil Biol. Biochem.*, 19, 187-193, 1987.
- Robertson, G. P., and J. M. Tiedje, Deforestation alters denitrification in a lowland tropical rain-forest, *Nature*, 336, 756-759, 1988.
- Rolston, D. E., D. L. Hoffman, and D. W. Toy, Field measurement of denitrification: I. Flux of N₂ and N₂O, *Soil Sci. Soc. Am. J.*, 42, 863-869, 1978.
- Ryden, J. C., N₂O exchange between a grassland soil and the atmosphere, *Nature*, 292, 235-237, 1981.
- Ryden, J. C., Denitrification loss from a grassland soil in the field receiving different rates of nitrogen as ammonium nitrate, *J. Soil Sci.*, 34, 355-365, 1983.
- Ryden, J. C., L. J. Lund, and D. D. Focht, Direct in-field measurement of nitrous oxide flux from soils, *Soil Sci. Soc. Am. J.*, 42, 731-737, 1978.
- Sahrawat, K. L., and D. R. Keeney, Nitrous oxide emission from soils, in *Advances in Soil Science*, vol. 4, edited by B. A. Stewart, pp. 103-148, Springer-Verlag, New York, 1986.
- Sanchez, P. A., *Properties and Management of Soils in the Tropics*, pp., Wiley Interscience, New York, 1976.
- Schimel, D. S., S. Simkins, T. Rosswall, A. R. Mosier, and W. J. Parton, Scale and the measurement of nitrogen gas fluxes from terrestrial ecosystems, in *Scales and Global Change*, SCOPE 35, edited by T. Rosswall, R. G. Woodmansee and P. G. Risser, pp. 179-193, John Wiley, New York, 1988.
- Schmidt, J., W. Seiler, and R. Conrad, Emission of nitrous oxide from temperate forest soils into the atmosphere, *J. Atmos. Chem.*, 6, 95-115, 1988.
- Seiler, W., and R. Conrad, Field measurements of natural and fertilizer induced N₂O release rates from soils, *J. Air Pollut. Control Assoc.*, 31, 767-772, 1981.
- Seiler, W., and R. Conrad, Contribution of tropical ecosystems to the global budgets of trace gases, especially CH₄, H₂, CO and N₂O, in *Geophysics of Amazonia: Vegetation and Climate Interactions*, edited by R. E. Dickinson, pp. 133-160, Wiley and Sons, New York, 1987.
- Sellers, P. J., Y. Mintz, Y. C. Sud, and A. Dalcher, A simple biosphere model (SiB) for use within general circulation models, *J. Atmos. Sci.*, 43, 505-531, 1986.
- Sextone, A. J., T. B. Parkin, and J. M. Tiedje, Temporal response of soil denitrification rates to rainfall and irrigation, *Soil Sci. Soc. Am. J.*, 49, 99-103, 1985.
- Shea, D. J., Climatological Atlas 1950-1979, Surface air temperature, precipitation, sea-level pressure and sea surface temperature (45°S-90°N), *Tech. Note NCAR/TN-269 + STR*, Atmos. Anal. and Pred. Div., Nat. Cent. for Atmos. Res., Boulder, Colo., 1986.
- Smith, C. J., R. D. Delaune, and J. W.H. Patrick, Nitrous oxide emission from Gulf Coast Wetlands, *Geochim. Cosmochim. Acta*, 47, 1805-1814, 1983.
- Tarpley, J. D., S. R. Schneider, and R. L. Money, Global vegetation indices from the NOAA-7 meteorological satellite, *J. Clim. Appl. Meteorol.*, 23, 491-494, 1984.
- Terry, R. E., I. R.L. Tate III, and J. M. Duxbury, The effect of flooding on nitrous oxide emissions from an organic soil, *Soil Sci.*, 132, 228-232, 1981.
- Thorntwaite, C. W., An approach toward a rational classification of climate, *Geogr. Rev.*, 38, 55-74, 1948.

- Tiedje, J. M., Ecology of denitrification and dissimilatory nitrate reduction to ammonium, in *Biology of Anaerobic Microorganisms*, edited by A. J. B. Zehnder, pp. 179-244, John Wiley, New York, 1988.
- U.S. Department of Agriculture, *Soil Taxonomy. A Basic System of Soil Classification for Making and Interpreting Soil USDA Surveys. Agr. Handb. 436*, Soil Conservation Service, U.S. Department of Agriculture, Washington, D. C., 1975.
- Van Diepen, C. A., Wetland soils of the world, their characterization and distribution in the FAO/Unesco approach, in *Wetland Soils: Characterization, Classification and Utilization*, Proceedings of IRRI Workshop, pp. 361-374, International Rice Research Institute, Los Baños, Philippines, 1985.
- Van Reeuwijk, L. P., Andosols, in *Lecture Notes on the Geography, Formation Properties and Use of the Major Soils of the World*, edited by P. M. Driessen and R. Dudal, pp. 57-65, Agricultural University, Wageningen and Katholieke Universiteit, Leuven, 1991.
- Vitousek, P. M., Nutrient cycling and nutrient use efficiency, *Am. Nat.*, 119, 553-572, 1982.
- Vitousek, P. M., Litterfall, nutrient cycling and nutrient limitation in tropical forests, *Ecology*, 65, 285-298, 1984.
- Vitousek, P. M., P. Matson, C. Volkman, J. M. Mass, and G. Garcia, Nitrous oxide flux from dry tropical forests, *Global Biogeochem. Cycles*, 3, 375-382, 1990.
- Vitousek, P. M., and P. A. Matson, Nitrogen transformations in a range of tropical forests, *Soil Biol. Biochem.*, 20, 361-367, 1988.
- Vitousek, P. M., and R. L. Sanford, Nutrient cycling in moist tropical forest, *Ann. Rev. Ecol. Syst.*, 17, 137-167, 1986.
- Watson, R. T., L. G. Meira Filho, E. Sanhueza, and A. Janetos, Sources and sinks, in *Climate Change 1992, The Supplementary Report to the IPCC Scientific Assessment*, edited by J. T. Houghton, B. A. Callander and S. K. Varney, pp. 25-46, Cambridge University Press, New York, 1992.
- Yoshida, T., and M. Alexander, Nitrous oxide formation by *Nitrosomonas europaea* and heterotrophic microorganisms, *Soil Sci. Soc. Am. J.*, 34, 880-882, 1970.
- Zimka, J. R., and A. Stachurski, Regulation of C and N transfer to the soil of forest ecosystems and the rate of litter decomposition, *Bull. Acad. Polish Sci.*, 24, 127-132, 1976.
- Zobler, L., A world soil file for global climate modeling, *NASA Tech. Memo. 87802*, 1986.
-
- A.F. Bouwman, National Institute of Public Health and Environmental Protection, P.O. Box 1, 3720 BA Bilthoven, The Netherlands.
- I. Fung, J. John, and E. Matthews, NASA Goddard Institute for Space Studies, 2880 Broadway, New York, NY 10025.

(Received April 20, 1992;
revised March 30, 1993;
accepted May 3, 1993.)